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COVER: Adult male Shikra (*Accipiter badius*). Painting by Lorenzo Starnini.

CONTENTS

A PARTIAL POST-JUVENILE MOLT AND TRANSITIONAL PLUMAGE IN THE SHIKRA (<i>ACCIPITER BADIUS</i>) AND GREY FROG HAWK (<i>ACCIPITER SOLOENSIS</i>). Marc Herremans and Michel Louette ..	249
TURNOVER AND DISPERSAL OF PRAIRIE FALCONS IN SOUTHWESTERN IDAHO. Robert N. Lehman, Karen Steenhof, Leslie B. Carpenter, and Michael N. Kochert	262
ROOST SITES OF RADIO-MARKED MEXICAN SPOTTED OWLS IN ARIZONA AND NEW MEXICO: SOURCES OF VARIABILITY AND DESCRIPTIVE CHARACTERISTICS. Joseph L. Ganey, William M. Block, and Rudy M. King	270
BARRED OWL AND SPOTTED OWL POPULATIONS AND HABITAT IN THE CENTRAL CASCADE RANGE OF WASHINGTON. Dale R. Herter and Lorin L. Hicks	279
FOOD HABITS OF BALD EAGLES WINTERING IN NORTHERN ARIZONA. Teryl G. Grubb and Roy G. Lopez	287
NEST FEATURES AND NEST-TREE CHARACTERISTICS OF SHORT-TOED EAGLES (<i>CIRCAETUS GALLICUS</i>) IN THE DADIA-LEFKIMI-SOUFLI FOREST, NORTHEASTERN GREECE. Dimitris E. Bakaloudis, Christos G. Vlachos, and Graham J. Holloway	293
ARE NORTHERN SAW-WHET OWLS NOMADIC? Jeffrey S. Marks and John H. Doremus	299
RELATIONSHIP BETWEEN RAPTORS AND RABBITS IN THE DIET OF EAGLE OWLS IN SOUTHWESTERN EUROPE: COMPETITION REMOVAL OR FOOD STRESS? David Serrano	305
AN EVALUATION OF METHYL ANTHRANILATE, AMINOACETOPHENONE, AND UNFAMILIAR COLORATION AS FEEDING REPELLENTS TO AMERICAN KESTRELS. Michael K. Nicholls, Oliver P. Love, and David M. Bird	311
SHORT COMMUNICATIONS	
RESPONSIVENESS OF NESTING EURASIAN KESTRELS <i>FALCO TINNUNCULUS</i> TO CALL PLAYBACKS. Luca Salvati, Alberto Manganaro, and Simone Fattorini	319
THE BREEDING SUCCESS OF TAWNY OWLS (<i>STRIX ALUCO</i>) IN A MEDITERRANEAN AREA: A LONG- TERM STUDY IN URBAN ROME. Lamberto Ranazzi, Alberto Manganaro, and Luca Salvati	322
NOCTURNAL ACTIVITY OF LESSER KESTRELS UNDER ARTIFICIAL LIGHTING CONDITIONS IN SEVILLE, SPAIN. Juan José Negro, Javier Bustamante, Ciro Melguizo, José Luis Ruis, and Juan Manuel Grande	327
NEST-SITE CHARACTERISTICS OF CRESTED CARACARAS IN LA PAMPA, ARGENTINA. Michael I. Goldstein	330
DIET OF THE BARN OWL (<i>TYTO ALBA TUIDARA</i>) IN NORTHWESTERN ARGENTINE PATAGONIA. Maria S. Pillado and Ana Trejo	334
LETTERS	339
BOOK REVIEW. Edited by Jeffrey S. Marks	342

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A PARTIAL POST-JUVENILE MOLT AND TRANSITIONAL PLUMAGE IN THE SHIKRA (*ACCIPITER BADIUS*) AND GREY FROG HAWK (*ACCIPITER SOLOENSIS*)

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ABSTRACT.—Molt has been poorly studied in the Accipitridae. Examination of museum specimens showed that there are three age-related plumages in the Shikra (*Accipiter badius*) and Grey Frog Hawk (*A. soloensis*) similar to the pattern known in the Levant Sparrowhawk (*A. brevipes*). The juvenile plumage with its distinctively-spotted underside is replaced by a transitional post-juvenile plumage during a partial contour molt between 4–10 mo of age. More feathers on the ventral side than on the dorsal side are replaced during this first contour molt, which is arrested at various stages of incomplete feather replacement. Usually, a significant part of the ventral pattern changes from spotted to barred, whereby the barring is on average more prominent than in adults. The early development of a transitional post-juvenile plumage might be related to early sex signaling. The adult plumage replaces the transitional post-juvenile plumage during a complete molt at about one year of age. In the subspecies *A. b. poliopsis* of the Shikra, which has almost no sexual dimorphism in the adult plumage, the transitional plumage is uncommon and very poorly developed.

KEY WORDS: *Shikra*; *Accipiter badius*; *Grey Frog Hawk*; *Accipiter soloensis*; *Levant Sparrowhawk*; *Accipiter brevipes*; *contour molt*; *transitional post-juvenile plumage*.

Muda parcial post juvenil y de transición de plumaje en *Accipiter badius* y *Accipiter soloensis*

RESÚMEN.—La muda ha sido poco estudiada en las Accipitridae. El examen de especímenes de museo demostró que hay tres plumajes relacionadas con la edad en *Accipiter badius* y en *A. soloensis* similar al patrón conocido en *A. brevipes*. El plumaje juvenil con su distintivo salpicado por debajo es remplazado por un plumaje de transición post juvenil durante una muda parcial entre los 4–10 meses de edad. Mas plumas del costado ventral que en el dorsal son remplazadas durante esta muda, la cual se detiene en varias etapas del reemplazo incompleto de plumas. Usualmente una parte insignificante del patrón ventral cambia de salpicado a barrado, en donde el barrado es en promedio mas prominente que en los adultos. El desarrollo temprano de un plumaje post juvenil de transición puede estar relacionado con señales sexuales tempranas. El plumaje adulto reemplaza al plumaje post-juvenil de transición durante una muda completa al año de edad. En la subespecie *A. b. poliopsis* la cual tiene un dimorfismo sexual en el plumaje adulto, el plumaje transicional es poco común y pobremente desarrollado.

[Traducción de César Márquez]

The molt of flight feathers has been studied in some species of *Accipiter* (e.g., *A. gentilis*, *A. nisus*, *A. cooperii*, *A. striatus*, *A. melanoleucus*, *A. badius*; Stresemann and Stresemann 1966, Hartley 1976, Fischer 1980, Newton and Marquiss 1982, Schmitt et al. 1982, Henny et al. 1985), but body molt is less well-documented. The larger goshawks gener-

ally undergo a complete molt taking several months during the second year of life (Hartley 1976, Fischer 1980). In the Eurasian Sparrowhawk (*A. nisus*), the best-studied species, adults molt during the breeding season in summer. Juveniles also undergo a complete molt that lasts several months during late summer and can continue into the sec-

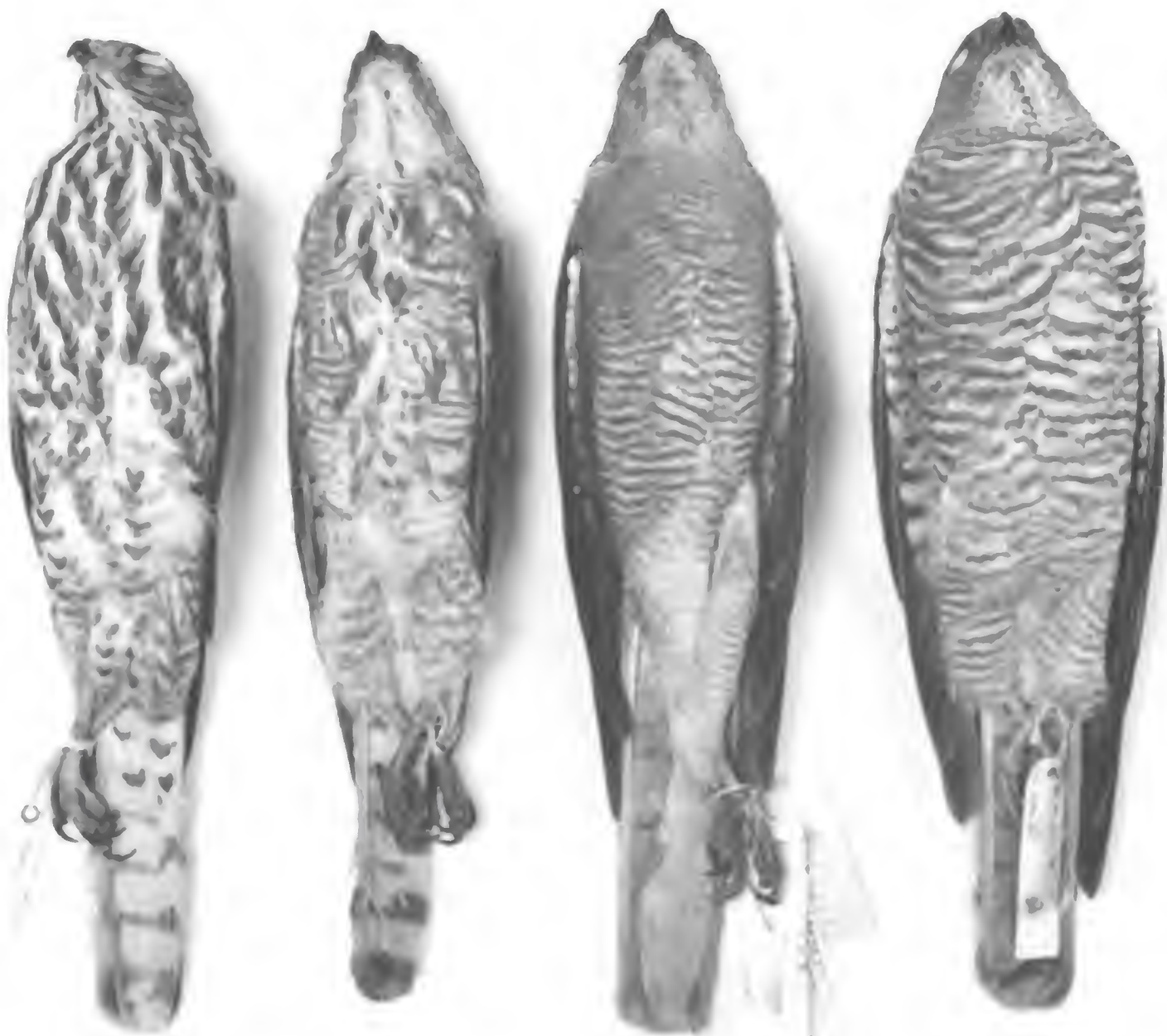


Figure 1. Ventral aspect of the plumages of the Levant Sparrowhawk (*Accipiter brevipes*). From left to right, juvenile (BMNH 1965.M.1087), October, Israel; transitional male (BMNH 1934.1.1.1221), June, Iran (note bold stripes remain from the juvenile plumage and tail feathers juvenile); adult male (BMNH 1956.57.13), May, Caucasus; adult female (BMNH 1934.1.1.1220), May, Iran. Photograph courtesy of the BMNH.

ond year of life (Stresemann and Stresemann 1960, 1966, Newton and Marquiss 1982). During this first molt, all the juvenile plumage is replaced by the adult plumage, except for the odd feather which allows one to identify second-year birds during the next year (Newton and Marquiss 1982). The migratory Sharp-shinned (*A. striatus*) and Cooper's (*A. cooperii*) Hawks similarly molt directly from the juvenile plumage to the adult plumage with a complete molt during the first summer after hatching (Mueller et al. 1979, 1981).

Like the European Sparrowhawk, adult Levant Sparrowhawks (*A. brevipes*) start a complete molt during the breeding season in summer and complete it in autumn, generally before migration

(Cramp and Simmons 1980, Forsman 1999). Juveniles, however, undergo a partial contour molt on the wintering grounds in Africa when only about six months old, and return to the breeding grounds in a transitional post-juvenile plumage. Adult plumage is acquired during a complete molt in summer at about one year of age; some birds carry over some juvenile feathers for the next molt (Cramp and Simmons 1980, Clark and Yosef 1998, Forsman 1999). The transitional plumage, which on the underside has a striking mixture of boldly streaked juvenile feathers and barred adult type feathers (Fig. 1; Clark and Yosef 1998, Forsman 1999) is kept only for about half a year, from winter until summer.

Molt information for the Shikra (*A. badius*) is scanty and contradictory. The Asian race *A. b. cenchroides* is said to follow the general pattern of the Eurasian Sparrowhawk (Cramp and Simmons 1980). Thiollay (1975) mentioned that *A. b. sphenurus* in the Ivory Coast only adopts adult plumage in the course of the second year. According to Friedmann (1930), there is an immature plumage with variable underside pattern, and Zimmerman et al. (1996) described an immature plumage resulting from a first molt. Verheyen (1953) rejected the existence of an immature plumage between juvenile and adult in *A. b. polyzonoides* in the Congo. Similarly, Schmitt et al. (1982) did not find any indication of an intermediate plumage in this race in South Africa, where the name Little Banded Goshawk is commonly used, despite the fact that they documented a partial post-juvenile contour molt.

The Shikra and Grey Frog Hawk (also called Chinese Goshawk; *A. soloensis*) are excellent species for the study the sequence of plumages on museum skins, because they have contrastingly different patterning on the underside between the juvenile and adult: boldly spotted and striped in the juvenile and finely barred (or mainly plain in the Grey Frog Hawk) in the adult. Tail feathers are boldly banded in juveniles, and particularly the inner and outer pair have reduced markings in the adult. Plumage classification is further facilitated by discrete breeding seasons, and discrete breeding and nonbreeding ranges in the Grey Frog Hawk. The migratory Grey Frog Hawk and the Asian races of the Shikra breed in spring (Ali and Ripley 1983), while in Africa the Shikra breeds late in the dry and early in the wet season, although this means in different months of the year at opposite sides of the equator (Elgood et al. 1973, Smeenk and Smeenk-Enserink 1977, Brown et al. 1982, Allan 1997). The extent of movements differs in the Shikra. The northcentral African race *A. b. sphenurus* is migratory in West Africa, where it moves north after breeding to molt (Elgood et al. 1973). It seems to be more resident in the eastern part of its range (Brown et al. 1982, del Hoyo et al. 1994). The southern African race *A. b. polyzonoides* does not undertake a regular migration, but is highly nomadic, particularly in the dry season (Allan 1997). Of the four Asian races, only the westernmost *A. b. cenchroides* is migratory (Blanford 1895, King et al. 1978, Ali and Ripley 1983, del Hoyo et al. 1994).

During work on plumages and ecology of some

African Accipiters (Louette 2000, Herremans et al. 2001), we became aware of the existence in several of the smaller species of a distinct transitional plumage, kept for a short period between the typical juvenile and adult plumage. Herein, we describe this transitional post-juvenile plumage in the Shikra and Grey Frog Hawk with reference to the similar and better-documented pattern in the Levant Sparrowhawk. We report on aspects of the molt sequence relevant to the development of the transitional plumage, and on its possible function.

METHODS

We examined the plumages of the Grey Frog Hawk at the Natural History Museum (BMNH), Tring, and studied the two African and four Asian subspecies of the Shikra in the Royal Museum for Central Africa (RMCA), Tervuren, and BMNH collections: 148 *A. b. polyzonoides* (southern Africa), 119 *A. b. sphenurus* (northcentral Africa), 150 *A. b. dussumieri* (India, Bangladesh), 115 *A. b. poliopsis* (northeastern India to Thailand and Vietnam), 43 *A. b. cenchroides* (Azerbaijan to northwestern India), and 32 *A. b. badius* (southwestern India, Sri Lanka). We noted the state of the plumage (juvenile/adult) separately for the contour feathers on uppersides, undersides, and rectrices and checked for active molt of primaries and tail feathers. Contour feather renewal was estimated in percent (mostly in steps of 10%) for the dorsal and ventral side separately. Sample sizes differed because some specimens were undated while, in others, the state of preparation precluded the assessment of contour molt extent, or limited extent in transitional birds precluded the comparison of ventral barring with that of adults.

RESULTS

Similar to the pattern that develops in the Levant Sparrowhawk, juveniles of the migratory Grey Frog Hawk undergo a partial body molt during their first winter in southeastern Asia and Wallacea. They replace a varying amount of contour feathers and return to the breeding grounds in China in a transitional, post-juvenile plumage with a mixture of juvenile and adult-type feathers, most conspicuous on the underside because of the differences in pattern: bold barring versus almost plain rufous-buff (Fig. 2). In general, the post-juvenile contour molt appears to advance in parallel on both ventral and dorsal sides. The average individual difference between the extent of renewal of ventral and dorsal feathers was insignificant ($0.25 \pm 3\%$ (\pm SE), range = -20% – 20% ; $N = 12$). We are not certain of timing of the complete molt in adults but it may terminate on the wintering grounds as evidenced by an undated adult from Jilolo Island (Moluccas) and two adults taken on Java that were growing outer primaries. However, an adult collected on 12



Figure 2. Ventral aspect of the plumages of the Grey Frog Hawk (*Accipiter soloensis*). From left to right, juvenile (BMNH 73.5.12.1593), no date, Batchian; transitional male (BMNH 1934.6.20.1), April, China (note underside predominantly boldly blotched and tail feathers juvenile); transitional male (BMNH 1903.7.3.94), May, China (note that fewer juvenile bars remain on lower underside and thigh feathers); adult female (BMNH 1905.12.24.955), May, China (note faintly barred on lower underside); adult male (BMNH 1914.5.1.69), March, China (plain rufous and white underside with marginal indication of barring). Photograph courtesy of the BMNH.

October in Thailand had old outer primaries but the others were newly-grown feathers, suggesting that most of the molt occurs during summer and autumn on the breeding grounds (immatures do normally return in transitional plumage to the breeding grounds, and it is unlikely that this bird had remained in its winter quarters). Adults may start molting on the breeding grounds, suspend molt during migration, and complete it in winter. The fact that some specimens showed a contrast between worn inner and new outer series of primaries seemed to confirm the existence of molt suspension.

In the southern African race of the Shikra (*A. b. polyzonoides*), the typical juvenile plumage (boldly marked below and brown with rusty edges above) was found unmolted from November–July (Table

1). Recently-fledged juveniles had been collected in November and January. From March onwards, some juveniles had molted body feathers. From May to October, body molt advancement showed great individual variation, but was never completed (Fig. 3). Because most birds examined had no growing feathers when collected, molt was apparently arrested before completion. Replacement of the juvenile plumage started on the ventral side with the upper throat. Molt on the upperside mostly started in the neck and the upper parts of the mantle, or on the head. In 44 of 47 transitional birds, replacement was more advanced on the ventral than dorsal side, while three birds had molted to a similar extent ventrally and dorsally. None of the birds that had replaced part of their juvenile plumage had already started to molt primaries or

Table 1. Monthly distribution (number of birds in collections studied) of plumage types and adult primary molt in subspecies of the Shikra (*Accipiter badius*).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	NO DATE
<i>A. b. polyzonoides</i> (<i>N</i> = 148)													
Juvenile	9	9	4	5	4	4	1	0	0	0	3	3	2
Transitional	0	0	2	9	11	9	5	1	7	3	0	0	6
Adult no molt	1	0	3	0	4	4	6	5	3	3	1	0	3
Adult molt	4	3	2	3	1	0	0	0	0	0	0	3	2
<i>A. b. sphenurus</i> (<i>N</i> = 119)													
Juvenile	0	1	1	4	1	5	6	6	2	0	3	0	0
Transitional	8	7	1	2	2	1	2	1	1	0	3	4	3
Adult no molt	6	3	5	5	5	2	0	1	1	2	3	7	1
Adult molt	0	0	0	0	2	2	2	4	1	1	1	1	0
<i>A. b. dassumieri</i> (<i>N</i> = 150)													
Juvenile	0	2 ^a	0	2 ^a	0	2	4	11	3	8	0	4	0
Transitional	5	3	3	2	2	0	0	2	3	5	6	3	4
Adult no molt	10	8	13	5	3	6	0	1	0	6	4	3	0
Adult molt	0	0	0	0	0	1	1	2	7	4	2	0	0
<i>A. b. poliopsis</i> (<i>N</i> = 115)													
Juvenile	13 ^a	5 ^a	3 ^a	3 ^a + 2	1	1 ^a + 4	5	1 ^a	3	1	4	8	0
Transitional	1	0	0	0	1	0	0	0	0	1	2	1	0
Adult no molt	11	3	3	2	3	0	0	0	0	10	3	6	0
Adult molt	0	0	0	0	0	3	1	3	6	0	0	0	0
<i>A. b. cenchroides</i> (<i>N</i> = 43)													
Juvenile	0	0	0	0	0	0	0	0	0	0	1	0	0
Transitional	0	1	1	0	1	0	0	0	0	0	1	1	0
Adult no molt	4	3	3	10	3	1	1	0	0	3	1	2	0
Adult molt	0	0	0	0	0	0	1	1	1	1	1	1	0
<i>A. b. badius</i> (<i>N</i> = 32)													
Juvenile	0	0	0	0	0	0	2	1	1	2	0	0	5
Transitional	1	0	1	0	0	0	0	0	0	0	0	0	3
Adult no molt	0	2	0	4	2	0	1	0	0	0	0	0	0
Adult molt	0	0	1	0	0	0	0	0	3	1	1	1	0

^a Very worn plumage, indicating that no molt to transitional plumage had taken place.

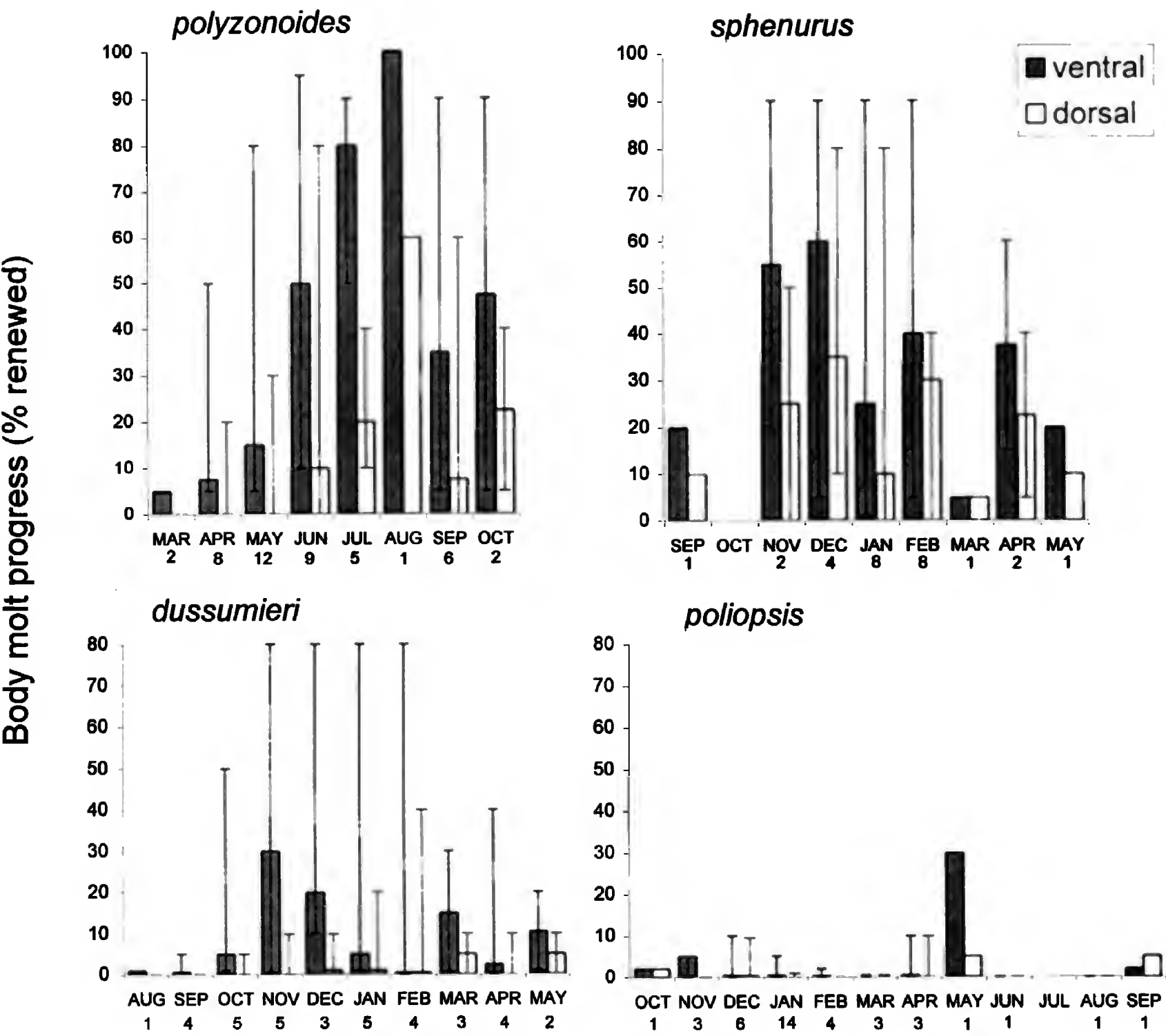


Figure 3. Progress of the post-juvenile body-molt on the dorsal and ventral side in subspecies of the Shikra (*Accipiter badius*). Monthly values for medians of ventral shown in dark bars, dorsal molt stage in white bars, and ranges in thin lines. Numbers under the figure indicate monthly sample sizes.

secondaries. One bird with well-advanced contour molt in June had new inner and outer tail feathers on both sides, but none growing. Most juveniles, therefore, acquire a transitional second plumage by a partial molt of the body feathers only, retaining most remiges and rectrices. The extent of this partial contour molt is highly variable individually (Fig. 3). A single second-year bird (BMNH 1910.7.1.108) was collected in November molting directly from a much-worn juvenile plumage to a fully adult plumage, apparently without having developed transitional plumage. Despite wide individual variation, the barring of the new feathers on

the ventral side of the transitional post-juvenile plumage tended to be broader and more rusty in color than in adults (Table 2; Fig. 4). Birds changed from transitional plumage into full, adult plumage through a complete molt when about 1 year old, almost synchronous with the molt of adults. Adults undergoing a complete molt from one definitive plumage to the next were collected from December (early stages) to May (latest stages). Recently-fledged young of *A. b. sphenurus* were dated February–September. Juveniles with transitional plumage appeared from September onwards (Table 1). The contour molt never completed, with

Table 2. Intensity of ventral barring of the transitional, post-juvenile plumage compared to adult plumage in subspecies of the Shikra (*Accipiter badius*).

	MEAN AD			
	P-J >	<P-J	MIN AD <	
	MAX AD ^a	< MAX	P-J <	P-J <
		AD ^b	MEAN AD ^c	MIN AD ^d
<i>A. b. polyzonoides</i>				
Males	6	5	5	0
Females	17	11	3	0
<i>A. b. sphenurus</i>				
Males	5	5	2	0
Females	8	4	4	0
<i>A. b. dussumieri</i>				
Males	7	8	2	0
Females	3	6	2	0

^a Barring of post-juvenile plumage heavier (broader and more contrasting) than the maximum barring in adults.
^b Barring of post-juvenile plumage in between the heaviest and average barring of adults.
^c Barring of post-juvenile plumage in between the average and weakest barring of adults.
^d Barring of post-juvenile plumage poorer developed than weakest barring of adults.

great variation in the extent of renewal among individuals (Fig. 3). In general, we suspect a tendency for a less extensive transitional plumage than in *A. b. polyzonoides* (Fig. 3). Of 30 transitional birds, 26 had molted more extensively ventrally than dorsally; three had progressed equally and one had the upperside more extensively molted. One second-year bird (RMCA 102759) was molting directly from a much-worn juvenile plumage to the adult plumage with a complete molt, apparently without having developed a transitional post-juvenile plumage. In it, the bars on the underside of the transitional plumage tended to be more strongly marked than those of adults (Table 2; Fig. 5). One bird collected in February and several more collected between May and September were undergoing a complete molt from transitional post-juvenile plumage to full adult plumage and, therefore, when about one year old. Adults undergoing complete molts from one adult plumage to another were collected from May (early stages) to December (latest stages).

In *A. b. dussumieri*, recently-fledged juveniles were dated June–July and juveniles in fresh plumage were found until October. From August onwards, birds started to develop transitional plum-

age (Table 1; Fig. 3). Despite the great individual variation in extent of the contour molt, replacement was less extensive than in the African races (Fig. 3). Four birds had very worn juvenile plumages in February and April, indicating that they would most likely not have developed transitional plumage, but would have molted directly from worn, juvenile plumage to adult plumage with a complete molt (Table 1), similar to the few examples in the other races mentioned above. All of 37 transitional birds had molted more extensively ventrally than dorsally. Again, new feathers of the transitional plumage tended to be more prominently barred than in the adult plumage (Table 2; Fig. 6). No transitional birds were found during the complete molt into adult plumage, but this molt is likely to be synchronous with that of adults, which occurs shortly after breeding, from June–November (Table 2).

In *A. b. poliopsis*, recently-fledged juveniles were dated April–September. Few juveniles developed transitional plumage, and if so, mostly did so to a small extent, making it sometimes difficult to distinguish between transitional molt and accidental feather replacement (Table 1; Fig. 3). When 6–12-mo old, most juveniles had heavily-worn, juvenile plumage, without any sign of transitional post-juvenile plumage (Table 1). Consequently, the barring of the transitional plumage could not be compared to that in the adult plumage. One juvenile (BMNH 87.11.1.165) was in complete molt in June, changing feathers directly from a very worn juvenile plumage to the adult plumage. All of the individuals with worn plumage that were collected from January–June (Table 1) were expected to follow the same pattern. Birds in transitional plumage underwent a complete molt to adult plumage in April, May, and August, possibly slightly earlier than the molt in adults, which occurred June–September, after breeding (Table 1).

Specimens of *A. b. cenchroides* and nominate *A. b. badius* were limited. Several specimens of both races were in transitional plumage (Table 1). Of five transitional *A. b. cenchroides*, one had 80% of the ventral plumage renewed by December, another 60% by February, and the remainder had <15% new feathers. All five transitional *A. b. badius* had >20% renewed feathers ventrally, and three had 70–90% renewed. The limited data suggested that, among the Asian races, *A. b. badius* may develop the most extensive transitional plumage, while molt extent in the migratory *A. b. cenchroides* ap-



Figure 4. Ventral aspect of the plumages of the Shikra (*Accipiter badius polyzonoides*). From left to right, juvenile male (BMNH 1911.12.23.430), January, Zambia; transitional female (BMNH 1950.50.125), April, Namibia (note limited replacement and new feathers more prominently barred than in adult); transitional female (BMNH 80.1.30.3), no date, Zambia (note only some barring from juvenile plumage remaining on flanks and thighs, juvenile tail, and replaced feathers on underside more prominently barred than in adult); adult female (BMNH 1932.5.10.598), March, Tanzania; adult male (BMNH 94.6.16.170), no date, Zambia. Photograph courtesy of the BMNH.

pears more similar to *A. b. dussumieri*. There were too few specimens to compare the post-juvenile barring with that of adults. Adults had been collected from nests with eggs in April for *A. b. cenchrroides*, and molt in adults also followed breeding in this race (Table 1). From the timing of appearance of juveniles in the population and molt in adults (Table 1), it appeared that the same molt pattern also applied to the nominate race *A. b. badius*.

DISCUSSION

In *A. brevipes*, *A. soloensis*, and *A. badius*, juvenile birds in nestling plumage have undersides with large rufous-brown spots and stripes, and broad barring on the flanks; the upperside has rusty brown edges to a generally dark brown plumage

and all tail feathers are heavily banded. A transitional plumage occurs in the second half of the first year of life during which time remiges, most of the rectrices, and most of the larger upper wing coverts are retained from the juvenile plumage, but between 4–10 mo of age some of the body feathers are replaced. New feathers on the upperside resemble the adult type, while those on the underside become barred with a tendency for wider, bolder barring than in adults. The extent of the partial contour molt is highly variable between individuals and taxa, and some juveniles do not develop transitional plumage at all, particularly those of the race *A. b. poliopsis* of the Shikra. In it, the transitional plumage is replaced by adult plumage during a complete molt when one year old, more or less synchronous with the complete molt of



Figure 5. Ventral aspect of the plumages of the Shikra (*Accipiter badius sphenurus*). From left to right, juvenile male (RMCA 109477), July, Ethiopia; transitional male (RMCA 102.759), May, Uganda (note some spots from juvenile plumage left, tail juvenile and heavily banded, and more distinctly barred underside than adult); adult male (RMCA 95921), August, D.R. Congo (note less distinctly barred than female and unmarked outer tail feathers); transitional female (RMCA 102.736), June, Kenya (note some spots left from juvenile plumage, tail juvenile and heavily banded, and more prominently barred than adult); adult female (RMCA 103.515), November, D.R. Congo (note more distinctly barred than adult male, but less than post-juvenile female, unmarked outer tail feathers).

adults. Adults are uniformly bluish-grey dorsally (dark slate in *A. b. soloensis*) and have barring on the underside (almost plain in *soloensis*); females are generally more prominently barred than males. At least some tail feathers of adults have reduced banding. Adult plumage is replaced by a complete molt following breeding.

We lack information on whether birds may or may not breed when 1 year old and in transitional plumage. In migratory species such as the Levant Sparrowhawk and Grey Frog Hawk, transitional birds migrate to the breeding grounds. Brown et

al. (1982) indicated that the Shikra might breed at one year of age, while Thiollay (1975) suggested that some birds do not breed at age one. Zimmerman et al. (1996) felt that the race *A. b. sphenurus* might breed in transitional plumage but no cases of it were observed in *A. b. polyzonoides* by Tarboton (2000).

Schmitt et al. (1982) found that half of the 20 juveniles caught in South Africa were undergoing solely a contour molt in April and May, most likely the partial contour molt of the post-juvenile plumage we report here. The fact that a bird they clas-

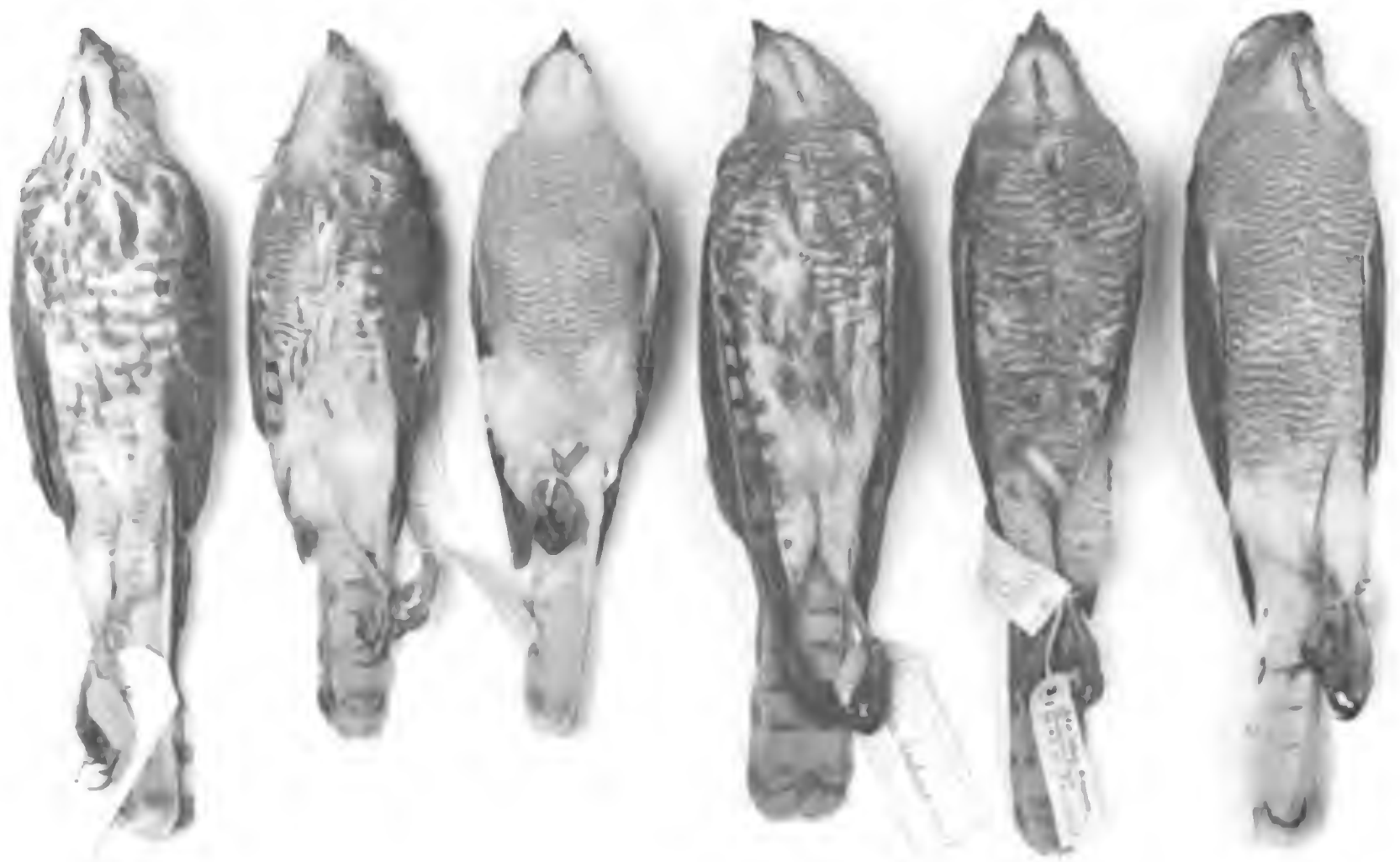


Figure 6. Ventral aspect of the plumages of the Shikra (*Accipiter badius dussumieri*). From left to right, juvenile female (BMNH 85.8.19.487), no date, India; transitional male (BMNH 85.8.19.481), October, India (note some spots from juvenile plumage left, tail juvenile and heavily banded, and more distinctly barred underside than adult); adult male (BMNH 1949.WHL.1.223), March, India (note underside less distinctly barred than female and unmarked outer tail feathers); transitional female (BMNH 85.8.19.508), March, Nepal (note many blotches left from the juvenile plumage, tail juvenile and heavily banded, and ventrally more prominently barred than adult); transitional female (BMNH 1949.25.87), November, Rawalpindi, Pakistan (note a few blotches left from the juvenile plumage and more prominently barred than adult); adult female (BMNH 86.3.25.79), December, India (note more distinctly barred than adult male but less than transitional female, and reduced markings on outer tail feathers). Photograph courtesy of the BMNH.

sified as a juvenile in May was recaptured a year later in adult plumage should not be seen as proof for the absence of an intermediate plumage. In fact, their observations fit exactly the plumage sequence we present here. A bird in recognizable juvenile plumage in May, whether or not the replacement of body feathers has started, is expected either to be in the transitional plumage or to have molted recently from the transitional to the adult plumage by next May. Schmitt et al. (1982) did not recognize the barred transitional plumage as different from the adult and, therefore, identified the bird as an adult when recapturing it a year later.

The individual they caught may have showed complete, adult plumage adding further evidence that the transitional plumage is retained for only about half a year and is replaced by the adult plumage in synchrony with the molt of breeding adults. We found several specimens for the different taxa molting from transitional plumage to adult plumage with a complete molt at about the same time as adults undergo the complete post-breeding molt. This meant that the transitional plumage is only worn for about half a year. Some transitional birds may molt slightly ahead of adults with non-breeding birds molting earlier.

If the transitional plumage is only retained for about half a year, are the feathers molted during the first year replaced again in the subsequent molt to adult plumage, or is all replacement part of the same molt cycle, with part of the contour molt shifted half a year forwards? Is the transitional plumage, therefore, a distinct plumage, or is it merely part of a protracted molt process? A pattern of a protracted molt with advanced contour molt would be similar to that found in several long-distance migrants (e.g., waders in the genus *Calidris*, Cramp and Simmons 1983) and in some swallows (*Hirundo* spp., *Delichon* spp., *Riparia* spp.) and warblers (*Acrocephalus* spp., *Locustella* spp., *Hippolais* spp., *Sylvia* spp., Jenni and Winkler 1994), which start a contour molt when still on the breeding grounds during the northern summer, but postpone the replacement of most remiges and rectrices of the same molt cycle until arrival on the wintering grounds some months later. In accipiters, if feathers of the transitional plumage are not replaced after half a year, there should be birds in the population with new, adult-type rectrices and two generations of contour feathers with undersides showing a mixture of worn, prominently barred feathers from the transitional plumage, and fresh, less barred, adult feathers. We have not found such birds in collections. Furthermore, because markings on the undersides of transitional birds were on average more prominent, we concluded that the molt at age one included all feathers. We found no evidence in the *Accipiter* literature of a possible split molt, whereby replacement of body feathers significantly precedes that of flight feathers during the same molt cycle. In the Eurasian Sparrowhawk, replacement of the primaries spans the entire molt period and no significant body molt occurs outside the period of primary replacement (Newton and Marquiss 1982). However, it has a rather variable plumage with poorly-differentiated adult and juvenile patterns (Nilsson 1992, Engström and Edelstam 1995). Although it is the best studied *Accipiter* species, it may thus be an unfortunate choice as the standard for the genus illustrating plumage sequences.

The transitional plumage in the three accipiters we studied clearly showed a separate, intermediate feather generation between juvenile and adult plumages (Humphrey and Parkes 1959). It results from its own, albeit partial and individually-variable contour molt, giving a plumage type which is different from that of adults.

Recently, a second-year plumage was described from the South American Gray-bellied Hawk (*A. poliogaster*), a species with a unique juvenile plumage (Whittaker and Oren 1999). We found a second-year plumage with broader ventral barring than in adults in the Mayotte subspecies of the Frances' Sparrowhawk (*Accipiter francesiae brutus*, Herremans et al. 2001). A transitional plumage, after a partial contour molt, is also more frequent in the Black-shouldered Kite (*Elanus caeruleus*) than previously known (Herremans 2000). The occurrence of early, partial post-juvenile molts in small raptors seems to be associated with a distinctive juvenile plumage with the underside pattern differing from that of adults. There are regions in the world where several accipiters, with essentially the same juvenile plumage co-occur (e.g., King et al. 1978, Zimmerman et al. 1996), and molt into a more adult-like plumage may be essential for proper species recognition before they can enter the breeding population. However, interspecific pressures may not be the main force behind the early molt, because the phenomenon also exists where no confusing juveniles of other species co-occur (e.g., on Mayotte Island: Herremans et al. 2001). At this point we are uncertain how it functions but the underside plumage is probably important in social communication in accipiters. Under this functional hypothesis, it is important that the adult-like ventral plumage be acquired before the start of the next breeding season. In the well-marked race of the Shikra (*A. b. poliopsis*), the sexual differentiation in ventral colors and patterning of adults is minimal and less than in the other races and the transitional, post-juvenile plumage is poorly developed. Possibly, the development of the transitional plumage functions as an early indication of the individual's sex and, because of the poor sexual plumage dimorphism of adults, there is no functional need for young *A. b. poliopsis* to change plumage at an early stage. Individual variation in the development of the post-juvenile molt might be dependent on condition and age, and the extent could also vary between years. Molt variation could, therefore, offer juveniles opportunities to advertise their sex, age, and individual quality. Age and quality have been demonstrated to have important impact on breeding performance in the Eurasian Sparrowhawk (Risch 1998), and it is likely that early advertisement of sex and quality for young birds entering their first breeding season is ultimately beneficial for their reproductive per-

formance. Under this hypothesis, aspects such as differences in territorial establishment, mating success, or recruitment into the breeding population at age one, may prove to be related to the extent of the post-juvenile molt.

Kemp (1999) demonstrated an early partial contour molt in the Greater Kestrel (*Falco rupicoloides*) which coincided with changes in territorial behaviors of adults. Small investments in a partial, post-juvenile molt, paralleled by changes in soft parts (e.g., eye color) resulted in important effects on communication and signaling. As in most accipiters, eye color changes with age in the Shikra from pale bluish-yellow in the fresh juvenile to yellow or orange in the transitional plumage and bright red in adults, with some variation according to sex and race. As in the Greater Kestrel, such changes in eye color could contribute to age and sexual communication in the Shikra.

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TURNOVER AND DISPERSAL OF PRAIRIE FALCONS IN SOUTHWESTERN IDAHO

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ABSTRACT.—We studied Prairie Falcon (*Falco mexicanus*) breeding dispersal, natal dispersal, and turnover at nesting areas in the Snake River Birds of Prey National Conservation Area (NCA) from 1971–95. Of 61 nesting areas where falcons identified one year were known to be present or absent the following year, 57% had a different falcon. This turnover rate was 2–3 times higher than that reported elsewhere for large falcons, and may have been related to high nesting densities in the NCA. Turnover at nesting areas was independent of nesting success in the previous year, but was significantly higher for females nesting on large cliffs. Mean distance between natal and breeding locations for 26 falcons banded as nestlings and later encountered as nesting adults was 8.9 km. Natal dispersal distances were similar for males and females, but more than twice as many males marked as nestlings were later encountered nesting in the NCA. Fourteen adult falcons found on different nesting areas in successive years moved an average of 1.5 km between nesting areas; males dispersed significantly farther than females. Natal and breeding dispersal distances in the NCA were lower than those reported for Prairie Falcons in other study areas. Only four falcons banded as nestlings were found outside NCA boundaries during the breeding period, and only one of these birds was known to be occupying a nesting area. We encountered no falcons banded outside the NCA occupying nesting areas in the NCA during this study.

KEY WORDS: *Prairie Falcon; Falco mexicanus; banding and marking; breeding dispersal; natal dispersal; nest-site fidelity; population turnover.*

Renovación y dispersión de *Falco mexicanus* en el suroeste de Idaho

RESÚMEN.—Estudiamos la dispersión reproductiva, la dispersión natal y la renovación en áreas de anidación en el Area Nacional de Conservación del Snake River (ANC), desde 1971–95. De las 61 áreas de anidación que fueron identificadas en un año y en las cuales los halcones estuvieron presentes o ausentes en el año siguiente, 57% tenían un halcón diferente. Esta tasa de renovación fue 2–3 veces mas alta que la reportada en otros sitios para halcones grandes, y pudo haber estado relacionada con las altas densidades en ANC. La renovación en las areas de anidación fue independiente del éxito de anidación en el año anterior, pero fue significativamente mayor para las hembras anidando en grandes riscos. La distancia media entre los sitios de reproducción y natalidad para 26 halcones anillados como pichones y posteriormente encontrados como adultos en anidación fue de 8.9 km. Las distancias de la dispersión natal fueron similares para machos y hembras; pero fueron mas del doble en los machos marcados como pichones que fueron encontrados anidando en la ANC. Catorce halcones adultos encontrados en distintas áreas de anidación en años sucesivos se desplazaron un promedio de 1.5 km entre áreas de anidación; los machos se dispersaron significativamente mas lejos que las hembras. Las distancias de la dispersión natal y reproductiva en la ANC fueron mas bajas que las reportadas para estos halcones en otras áreas de estudio. Solo cuatro halcones anillados como pichones fueron encon-

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trados por fuera de los límites de la ANC durante el período reproductivo y tan solo una de estas aves ocupó el área de anidación. No encontramos ningún halcón anillado por fuera de la ANC ocupando algún área de anidación durante este estudio.

[Traducción de César Márquez]

Many raptor nesting areas are occupied year after year, but usually it is not known whether the same individuals occupy the same nesting areas in successive years (Newton 1979). Fidelity to nesting areas varies among species and populations. Small species with short life spans and those that occupy unpredictable environments are less likely to be sedentary than large, long-lived species occupying stable habitats (e.g., James et al. 1989, Jenkins and Jackman 1993, Rosenfield and Bielefeldt 1996). Within populations, older birds, successful breeders, and birds occupying high quality nesting areas often are more faithful to their nesting areas in successive years (Newton 1986, Village 1990, Foreiro et al. 1999). In most bird species, females move farther from the natal site to breed, change nesting locations more often, and move greater distances between nesting areas used in different years than males (Greenwood 1980, Greenwood and Harvey 1982).

Few data are available on Prairie Falcon (*Falco mexicanus*) turnover and dispersal. Steenhof et al. (1984) reported natal dispersal data for southwest Idaho for the 1970s and early 1980s, and Runde (1987) reported turnover and dispersal data for study areas in Wyoming, Colorado, and Alberta. Since the early 1980s, more than 1000 Prairie Falcons have been marked in the Snake River Birds of Prey National Conservation Area (NCA) in southwest Idaho, providing an opportunity for a more thorough analysis of turnover and dispersal than was possible in 1984. We were particularly interested in whether patterns of dispersal were related to gender, environmental factors, or reproductive success, and whether patterns in the NCA were similar to those in other study areas. We hypothesized that female falcons would exhibit higher turnover rates and disperse farther than males, and that turnover rates would be highest at nesting areas that failed to produce young in the previous year. We also expected turnover rates to be high at nesting areas with low long-term occupancy rates and at those on large cliffs, where potential nest sites were abundant.

STUDY AREA

The NCA comprises 196 225 ha of canyonlands and shrubsteppe desert adjoining the Snake River in south-

western Idaho (USDI 1995). Our study focused on a 130-km stretch of the Snake River Canyon extending from Walters Ferry on the west to Hammett on the east. This area supports the densest known nesting concentration of Prairie Falcons (USDI 1979). During years when full counts of nesting pairs were obtained (1976–78, 1990–94), numbers ranged from 160 to 206 (Steenhof et al. 1999). In parts of the NCA where falcon densities are highest, canyon walls reach 125 m in height and often stretch uninterrupted for many kilometers. In these areas, falcons typically nest <200 m and occasionally <50 m from other pairs (Steenhof 1998). In other parts of the NCA, nesting pairs may be up to 5 km apart. Prairie Falcons leave the NCA soon after young fledge and migrate to widely separated post-nesting and wintering areas, primarily east and south of the NCA (Steenhof et al. 1984).

METHODS

Marking. From 1970–94, 2060 Prairie Falcons were banded in the NCA primarily during two periods of intensive research (USDI 1979, 1996), and as part of annual monitoring efforts (Table 1). All falcons were banded with U.S. Fish and Wildlife Service (FWS) leg bands, and 1189 birds also received colored leg bands, patagial markers (Kochert et al. 1983), and/or radio-transmitters (USDI 1979, Vekasy et al. 1996, Marzluff et al. 1997), depending on research objectives (Table 1). Adults were trapped between March and June each year, and nestlings were banded in May and June, just before fledging. We applied several types of colored leg bands, particularly during the late 1980s and 1990s. Plastic bands were used in 1977 and 1986, and anodized aluminum bands were used in 1987 and from 1990–94. From 1986–94, all color bands were inscribed with a unique alpha-numeric code.

Data Collection. We defined a historical nesting area as any area of cliff where a Prairie Falcon pair was found in one or more years but where no more than one pair nested in the same year (Newton and Marquiss 1982). From 1973–95, we mapped 317 historical nesting areas based on records of 3170 nesting attempts. Delineated areas included scrapes, perches, and defended areas. We defined an encounter as a determination of a bird's FWS band number or alpha-numeric code by any means (Harmata et al. 1999). During most years, data collection was incidental to other research and monitoring efforts (see Steenhof et al. 1999 for methods). However, the intensive field efforts conducted in the late 1970s and early 1990s provided more opportunities to encounter marked birds than in other years. In 1995, efforts to locate and identify marked birds were more systematic. That year, we tried to identify falcons at all nesting areas where falcons had been radiotagged in 1994, by trapping adults or reading band numbers from a distance. If 1994 occupants were not present in their nesting areas in 1995, we searched for them in the two nearest nesting areas (typically the

Table 1. Number of Prairie Falcons marked in the NCA, by year and age class, 1970–94. Columns give the number banded with FWS leg bands. Additional markers (number and type) are given in parentheses (P = patagial tag, R = radiotransmitter, C = colored leg band).

YEAR	NESTLINGS BANDED	ADULTS BANDED	TOTALS
1970	16	0	16
1971	110	0	110
1972	142	0	142
1973	0	0	0
1974	41	0	41
1975	79 (8P, 7R)	3 (3R)	82
1976	151 (107P, 9R)	8 (2P, 6R)	159
1977	118 (10P, 32C)	11 (5C, 4R)	129
1978	104 (74P)	14	118
1979	75 (57P)	0	75
1980	79	0	79
1981	7	0	7
1982	4	0	4
1983	19	0	19
1984	68	0	68
1985	0	0	0
1986	25 (25C)	0	25
1987	104 (91C)	0	104
1988	0	1	1
1989	0	0	0
1990	80	20 (20C, 18R)	100
1991	154 (148C)	29 (28C, 28R)	183
1992	213 (195C, 79R)	34 (33C, 31R)	247
1993	118 (116C, 73R)	49 (42C, 38R)	167
1994	151 (147C)	33 (33C, 32R)	184
Total	1858	202	2060

adjacent upstream and downstream sites). During most years, we used binoculars and 15–60× spotting scopes to observe falcons. From 1991–95, we also used a 160× Questar telescope to read alpha-numeric codes on colored leg bands.

Turnover. We estimated turnover as the proportion of nesting areas occupied in successive years where marked adults identified the first year were not present the following year. We considered that turnover occurred if a different individual was trapped during the second year; if a bird’s color band inscription did not match that of the previous occupant; if a bird’s band color or placement differed from that of the previous occupant; if the new occupant was unmarked; or if the previous occupant was encountered in another nesting area or was found dead. We used nesting areas more than once in the analysis if the same occupant was identified in more than two consecutive years or if both occupants were marked in the same year. Nesting areas that were vacant the year after birds were marked were not used in the analysis.

To assess factors that might influence turnover, we classified nesting areas according to nesting success in the year before turnover was assessed, long-term occupancy,

and cliff height. We considered a nesting area successful if ≥1 young reached 30 d of age (Steenhof 1987). We based occupancy rates on the proportion of years that pairs were present at nesting areas in our sample during 8 yr when full surveys of the NCA were conducted (1976–78, 1990–94) (Steenhof et al. 1999). We classified nesting areas that had pairs present ≤65% of years ($N = 10$) as low occupancy sites. Those with pairs present >65% of years ($N = 36$) were classified as high occupancy sites. We computed cliff-height categories at nesting scrapes from studies that interpreted aerial photographs using standard parallax methods (Bentley and Hardyman unpubl. data). We considered cliffs ≤30.6 m to be small and those >30.6 m to be large. These categories reflected the fact that most cliffs in the NCA are under 30.6 m in height, but higher cliffs often reach 125 m.

Dispersal. We calculated natal and breeding dispersal distances from Universal Transverse Mercator coordinates assigned to banding and encounter locations. To assess natal dispersal, we recorded all cases where falcons marked as nestlings were encountered later as breeding adults. To assess breeding dispersal, we recorded all cases where breeding adults were encountered in different nesting areas in subsequent years, including birds banded as nestlings if they moved to different nesting areas after we found them breeding. We measured distances between nesting scrapes if known, or between centers of nesting areas if locations of nesting scrapes were unknown. We also counted the number of historical nesting areas between nesting areas used by the same falcon.

Data Analysis. We ran all statistical tests using SAS software (SAS Institute Inc. 1990). Because our investigation was exploratory in nature and our sample sizes were small, we opted to increase power and reduce the risk of Type II errors by considering P -values ≤0.10 as significant. We used contingency table analysis (G -tests) to assess gender differences in turnover and in the tendency of falcons to breed near their natal areas. We also used G -tests to relate turnover to nesting success in the previous year, cliff height, and long-term occupancy. Because dispersal data were not normally distributed, we used the Wilcoxon rank sums test, a nonparametric alternative to the t -test, to assess differences in natal and breeding dispersal distances. We identified gender of nestling and adult falcons using foot pad length at the time they were banded (Marzluff et al. 1991) and copulatory behavior observed after release. Birds with foot pads <86 mm were considered to be males; those with foot pads >86 mm were considered to be females.

RESULTS

Encounters with Marked Birds. We recorded 76 encounters with 63 marked falcons (34 males and 29 females) at 46 nesting areas during breeding seasons from 1976–95. Sixty-five encounters occurred between 1990–95. Twenty-six (41%) of 63 individuals encountered were marked as nestlings, and 37 (59%) were marked as breeding adults. We recorded more than one encounter with 12 birds: 11 falcons were recorded at nesting areas in two

Table 2. Status and turnover at Prairie Falcon nesting areas in the NCA one year after they were occupied by marked adults, 1975–94.

	NUMBER OF NESTING AREAS				TURNOVER
	SAME BIRD	DIFFERENT BIRD	UNKNOWN OCCUPANT	VACANT	
Males	11	11	51	24	50%
Females	15	24	55	28	61%
Both sexes	26	35	106 ^a	52	57%

^a Includes 4 nesting areas for which occupancy was not confirmed the following year.

different years after they were banded, and one bird was seen in three different years.

Turnover. We evaluated 219 nesting areas where marked adults were known to be present in at least one nesting season from 1970 to 1994. Of these, 102 were occupied the following year by falcons we did not check for identity, 52 were vacant, and occupancy was unconfirmed for 4 (Table 2). This left 61 cases for turnover assessments. Of these, 26 had the same bird and 35 had a different bird the following year. Thus, turnover was 57% for both sexes combined. Turnover was similar for males (50%) and females (61%) ($G_1 = 0.76$, $P = 0.38$).

Of 35 nesting areas where turnover of marked birds occurred, 18 were occupied by new individuals with known band numbers, and 17 were occupied by unidentified birds. In the latter 17 cases, we knew turnover occurred because eight previous occupants were on different nesting areas, six new occupants were unbanded, two new occupants wore different colored bands than those of the previous occupant, and one previous occupant was found dead soon after its first encounter. We were able to account for only one missing bird from the 18 nesting areas where new birds were identified. This bird was found dead near its former nesting area early in the second breeding season.

Sample sizes were inadequate to assess annual turnover for most years. However, in 1995 we confirmed if marked birds had returned to their former nesting areas in 19 cases. Of these, seven nesting areas (37%) were occupied by the same individual, and 12 nesting areas (63%) were occupied by a different bird. This turnover rate (63%) did not differ from that of all other years (55%) ($G_1 = 0.38$, $P = 0.54$).

Turnover of marked falcons was independent of nesting success in the previous year and long-term occupancy of the nesting area. New birds appeared at 4 of 10 nesting areas with low long-term occu-

pancy rates (40%), compared to 31 of 51 nesting areas with high occupancy rates (61%) ($G_1 = 1.46$, $P = 0.30$). Turnover occurred at 19 of 32 successful nesting areas (59%), compared to 10 of 18 unsuccessful nesting areas (56%) ($G_1 = 0.07$, $P = 0.79$).

When we considered relationships between turnover and nesting success in the previous year and turnover and long-term occupancy by sex, we found no differences for males or females ($G_s \leq 2.50$, $P_s \geq 0.11$). However, cliff height was related to female but not male turnover. Only 3 of 14 females returned to nesting areas on large cliffs, compared to 12 of 25 females on small cliffs ($G_1 = 2.80$, $P = 0.09$).

Site Fidelity. At least 26 falcons returned to their former nesting areas the year after they were marked or last seen (Table 2). Of these, two females returned to the same nesting area for a third consecutive year. Both birds occupied their nesting areas from 1977–79. The 26 falcons also included a male that returned to the same nesting area for two consecutive years and one nonconsecutive year. This bird, banded as a nestling in 1990, was found at a nesting area >14.2 km downstream from its natal area in 1991, 1992, and 1994. It likely occupied this same nesting area in 1993, but identification was inconclusive. In 1995, it was replaced by a marked, 1-yr-old male. Five other individuals (3 males and 2 females), not included in the sample of 26 falcons described above, were found in the same nesting areas in two nonconsecutive years.

Natal Dispersal. Of 1858 Prairie Falcons banded as nestlings (Table 1), 26 (1.4%) were encountered during subsequent breeding seasons. These 26 falcons were 1–5-yr old when encountered on nesting areas (Table 3). More than twice as many males ($N = 18$) were encountered as females ($N = 8$) ($G_1 = 2.01$, $P = 0.08$).

Distances between natal areas and breeding sites

Table 3. Natal dispersal distances (km) of Prairie Falcons marked as nestlings between 1972–94 that returned to occupy nesting areas in the NCA as breeders.

AGE IN YEARS	MALES ^a		FEMALES ^b		BOTH SEXES		
	NO. BIRDS	MEAN ± SD	NO. BIRDS	MEAN ± SD	NO. BIRDS	MEAN ± SD	RANGE
1	3	12.3 ± 8.1	0		3	12.3 ± 8.1	3.4–19.3
2	6	5.6 ± 4.4	1	5.8	7	5.6 ± 4.0	1.1–13.0
3	4	19.0 ± 14.9	2	8.2 ± 2.1	6	15.4 ± 12.8	6.3–35.6
4	4	6.7 ± 5.0	5	5.6 ± 2.9	9	6.1 ± 3.7	1.7–14.1
5	1	8.3	0		1	8.3	
Total	18	10.1 ± 9.3	8	6.2 ± 2.6	26	8.9 ± 8.0	1.1–35.6

^a Range (all males): 1.1–35.6.
^b Range (all females): 1.7–9.8.

were similar for males (\bar{x} = 10.1 km; median = 6.35 km; range = 1.1–35.6 km) and females (\bar{x} = 6.2 km; median = 5.9 km; range = 1.7–9.8 km) (S = 98; P = 0.59) (Table 3). Numbers of historical nesting areas between natal and breeding sites for males (\bar{x} = 24.4; range = 2–95) and females (\bar{x} = 19.6; range = 5–44) also were similar (S = 101; P = 0.72). In three cases where we had dispersal data on closely related individuals, distances and direction moved were similar (Table 4).

Four falcons banded as nestlings in the NCA were encountered as yearlings outside the NCA during the breeding season (Steenhof et al. 1984). These birds were encountered in northern Idaho, western Montana (>300 km from the natal areas in both cases), eastern Oregon (101 km from the natal area), and southern Idaho (41–116 km from the natal area). Only the bird in southern Idaho was known to be occupying a nesting area at the time of the encounter; however, it was not identified to individual, so we could not determine the exact distance it dispersed.

Breeding Dispersal. We recorded 20 encounters with marked adults in different nesting areas one or more years after their last known breeding location. None of these encounters occurred outside the NCA. Falcons found one year later (N = 14) moved an average of 1.5 km (Table 5). Males dispersed significantly farther (\bar{x} = 3.3 km; median = 2.75; range = 1.5–6.2 km) than females (\bar{x} = 0.7 km; median = 0.5; range = 0.1–1.9 km) (S = 49, P = 0.009). When we included six falcons (a female and 5 males) encountered two to three years after their last known nesting location, mean distance between nesting areas increased to 2.0 km (Table 5). With movements in nonconsecutive years included, dispersal distances of males were still greater than females (S = 117, P = 0.09).

Of 20 individuals encountered in new nesting areas one or more years after they were last identified, 10 (2 males and 8 females) moved to adjacent nesting areas. The remaining 10 individuals (5 males and 5 females) crossed 1–28 nesting areas (\bar{x} = 7.5) during dispersal movements. Males (\bar{x} =

Table 4. Natal dispersal of related individuals in the NCA. All birds shown were banded as nestlings.

RELATIONSHIP	YEAR BANDED	YEAR ENCOUNTERED	DIRECTION MOVED	DISTANCE MOVED (km)
Brother	1987	1990	Southeast	27.5
Sister	1987	1991	Southwest	1.7
Brother	1990	1991	Northwest	14.2
Brother	1990	1992	Northwest	13.0
Father	1987	1990	Southeast	6.5
Son	1990	1992	Southeast	4.8
Son	1990	1993	Southeast	6.3

Table 5. Breeding dispersal distances (km) for Prairie Falcons that moved from a previous year's nesting area. Sample size is in parentheses.

	SEX	MEAN DISPERSAL	
		DISTANCE ± SD	DISPERSAL RANGE
Consecutive years	Male	3.3 ± 2.0 (4)	1.5–6.2
	Female	0.7 ± 0.6 (10)	0.1–1.9
	Both	1.5 ± 1.6 (14)	0.1–6.2
All encounters	Male	3.4 ± 4.5 (9)	0.2–14.4
	Female	0.8 ± 0.7 (11)	0.1–1.9
	Both	2.0 ± 3.2 (20)	0.1–14.4

11.0; range = 1–28) and females (\bar{x} = 4.4; range = 1–7) crossed similar numbers of nesting areas during these movements (S = 31.5, P = 0.46).

Of 26 falcons that returned to the same nesting areas in consecutive years, five used the same nesting scrape as the previous year. Of 21 falcons found in the same nesting areas but in different nesting scrapes, 17 moved <0.5 km. The other four falcons moved 0.5–0.8 km. When these falcons were included in estimates of breeding dispersal, mean dispersal distance for encounters in consecutive years dropped to 0.8 km: 1.2 km for males (N = 13), and 0.5 km for females (N = 22).

DISCUSSION

Turnover. Turnover for Prairie Falcons in the NCA was 2–3 times higher than rates reported in other studies of large falcons (Mearns and Newton 1984, Runde 1987, Court et al. 1989). High turnover rates in the NCA may be due partly to high falcon densities. Mean density of nesting pairs throughout the NCA is 0.7 pairs per linear km, and densities reach 4.3 pairs per km in areas where cliffs exceed 100 m in height (Steenhof 1998). Most nesting areas where we studied turnover were in the deepest parts of the canyon; thus, densities in our study area were more than 4 times those reported elsewhere. The highest mean densities recorded for Prairie Falcons in other study areas were 0.6 pairs per km in southwestern Wyoming (Runde 1987), and 0.3 pairs per km on the Kevin Rim, Montana (Harmata et al. 1991). Density may affect turnover by influencing the availability of potential mates. Where densities are low, returning to a previous breeding area may be the most effective means of finding a mate. Where densities are high, abundance of potential mates may reduce a

falcon's need to return to a specific former nesting area.

High turnover in the NCA also may be related to the abundance of nest sites in the area, and the fact that nesting cliffs tend to be continuous. Each year, many historical nesting areas in the NCA are unoccupied. No more than 206 Prairie Falcon pairs have been recorded nesting in the NCA in any given year (Steenhof et al. 1999), yet 317 historical nesting areas have been identified. Where nest sites are abundant and distances between alternate sites are low, frequent moves to different nesting locations might be expected.

Other factors may affect turnover in large falcons, including gender, previous nesting success, long-term occupancy, and nest site or mate quality. The fact that females tended to move more often than males is consistent with studies that suggest turnover in large falcons is slightly higher for females (Runde 1987, Enderson and Craig 1988, Court et al. 1989). In this respect, our data are consistent with overall trends in birds (Greenwood 1980, Greenwood and Harvey 1982). However, our data are inconsistent with other studies in two respects. In Eurasian Sparrowhawks (*Accipiter nisus*) and Eurasian Kestrels (*Falco tinnunculus*), turnover was lower for birds that nested successfully the previous year, and for those from nesting areas with high long-term occupancy rates (Newton 1986, Village 1990). In the NCA, birds from previously successful nesting areas and nesting areas with high long-term occupancy rates showed no greater tendency to return than birds from unsuccessful nesting areas and nesting areas with low long-term occupancy; but females nesting on large cliffs were more likely to move than those on small cliffs. Our results again may be related to the abundance of ledges, cavities, and potential mates in the NCA. Falcons from some previously successful nesting areas may have been displaced by other individuals seeking higher quality sites or better mates, or some falcons may have moved to better nesting areas. The abundance of potential partners and places to nest made it likely that individuals displaced from former nesting areas would find other breeding opportunities.

Dispersal. Both natal and breeding dispersal distances in the NCA were shorter than previously reported for Prairie Falcons (Runde 1987). As in most studies of dispersal, the natal and breeding dispersal distances we recorded may be biased downward because we did not search for marked

birds outside the NCA. Furthermore, our searches for marked birds focused on previously used and adjacent nesting areas. Thus, we were more likely to find birds within a few kilometers of their natal or previous breeding sites. This bias may partly explain why both our natal and breeding dispersal distances were shorter than for Alberta, Colorado, and Wyoming (Runde 1987).

As with turnover, population density and habitat features also could explain shorter dispersal distances in the NCA. Falcons do not need to travel far to find nesting sites or mates in the NCA because stretches of cliff tend to be continuous and potential mates are abundant. In other parts of western North America, nesting cliffs are widely scattered and nesting pairs are clumped, typically with <10 pairs on individual buttes or escarpments (Runde pers. comm., Harmata et al. 1991). Birds that do not return to their natal or former nesting areas have fewer alternative sites available for nesting and fewer mate choices. Those that leave the local area to find breeding opportunities must travel greater distances.

In contrast to Runde's (1987) findings and the predictions of Greenwood (1980) and Greenwood and Harvey (1982), natal dispersal distances for females in the NCA were not longer than males. However, if females dispersed outside the NCA, we would not have found them and recorded the distances. Although our encounter rate likely underestimates the total number of returning birds, it is relatively unbiased with respect to gender because we banded similar numbers of males (923) and females (935) as nestlings and we trapped similar numbers of adult males (90) and females (100) as breeders. Thus, our findings suggest that males were more likely than females to return to breed in the NCA and are consistent with predictions of female-biased dispersal in raptors.

The fact that we encountered few birds marked as nestlings in later years is partly an artifact of our failure to check for birds at all nesting areas, and should not be construed as evidence for frequent emigration. Low encounter rates also may be related to high post-fledging mortality in the NCA (McFadzen and Marzluff 1996). Short natal and breeding dispersal distances, and the fact that only one falcon banded inside the NCA is known to have nested outside NCA boundaries, may indicate that very little dispersal from or into the NCA occurs. However, because many falcons inside the NCA in any given year were unmarked, and be-

cause we conducted no searches for marked falcons outside the NCA, conclusions regarding the extent of falcon immigration into and dispersal from the NCA must remain tentative.

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ROOST SITES OF RADIO-MARKED MEXICAN SPOTTED OWLS IN ARIZONA AND NEW MEXICO: SOURCES OF VARIABILITY AND DESCRIPTIVE CHARACTERISTICS

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ABSTRACT.—To increase understanding of roosting habitat of Mexican Spotted Owls (*Strix occidentalis lucida*) and factors that influence use of roosting habitat, we sampled habitat characteristics at 1790 sites used for roosting by 28 radio-marked Mexican Spotted Owls in three study areas in Arizona and New Mexico. We explored potential patterns of variation in roost-site characteristics by estimating similarity among all possible pairs of roost sites and summarizing patterns in these similarity estimates using a linear model. Factors in the model included owl identity and season. We conducted these analyses within study areas, because habitat characteristics differed among study areas. We used a repeated-measures model which assumed that similarity estimates computed between roost sites of the same owl or pairs of owls were correlated. This model significantly improved model goodness-of-fit over a null model assuming no such correlation structure. Similarity estimates were relatively high (0.744–0.775) in all three study areas, suggesting consistent patterns of selection among owls within areas. Owl and season effects were relatively small but detectable in all study areas, with the relative magnitude of these effects differing among areas. The seasonal effect was greatest in the area dominated by pine-oak forest and relatively slight in two areas where owls roosted primarily in mixed-conifer forest. Relative to areas where owls roosted in mixed-conifer forest, roosts in pine-oak forest occurred on moderate slopes, on southwest to northwest aspects, and were less concentrated on lower portions of slopes. We suspected that much of this difference reflected differences in stand-development processes in different forest types. This suggested that land managers should incorporate knowledge of such patterns in different forest types and topographic locations in planning decisions involving management of Spotted Owl habitat.

KEY WORDS: *Mexican Spotted Owl*; *Strix occidentalis lucida*; Arizona; New Mexico; radiotelemetry; repeated measures; roost sites; sources of variation.

Sitios de perchas de *Strix occidentalis lucida* marcados con radio-transmisores en Arizona y Nuevo México: fuentes de variabilidad y características descriptivas

RESÚMEN.—Para aumentar el conocimiento de los habitats de perchas de *Strix occidentalis lucida* y los factores que influyen en su uso, muestreamos las características del habitat en 1790 sitios utilizados como perchas por 28 buhos con radio transmisores en tres areas de estudio en Arizona y Nuevo México. Exploramos los patrones de variación dentro de las características mediante la estimación de la similaridad entre todos los posibles pares de sitios de perchas y resumimos los patrones dentro de estos estimativos de similaridad utilizando un modelo lineal. Los factores en el modelo incluyeron la identidad de los buhos y la epoca. Condujimos estos análisis dentro de las áreas de estudio debido a que las características de habitat difirieron entre las áreas de estudio. Utilizamos un modelo de repetición de medidas el cual asumió que las estimaciones de similaridad estimadas computados entre los sitios de perchas de las mismas parejas de buhos estaban correlacionadas. Este modelo mejoró significativamente al modelo de bondad de ajuste sobre el modelo nulo, asumiendo la correlación de estructura. Los estimativos de similaridad fueron relativamente altos (0.744–0.775) en las tres áreas de estudio, sugiriendo patrones consistentes de selección entre buhos y dentro de las areas. Los efectos de buhos y estación fueron relativamente pequeños pero detectables en todas las areas de estudio, con una magnitud relativa de estos efectos diferidos entre áreas. El efecto de la estacionalidad fue mayor en el área dominada por los bosques de roble y relativamente pequeño en las dos áreas en donde los buhos se percharon principalmente en bosques de coníferas mixtas. Con relación a las áreas en donde los buhos

se perchó en bosques mixtos de coníferas, las perchas en los bosques de robles y pinos ocurrieron en vertientes moderadas en el suroeste y noroeste, estas fueron menos concentradas en la porción baja de las vertientes. Sospechamos que buena parte de esta diferencia es producto del proceso de desarrollo de árboles en distintos tipos de bosques. Esto sugiere que los planificadores deben incorporar el conocimiento de estos patrones en diferentes tipos de bosques y situaciones topográficas en las decisiones de planificación que involucran el manejo de habitat de los buhos.

[Traducción de César Márquez]

The Mexican Spotted Owl (*Strix occidentalis lucida*) occurs throughout the southwestern United States and northern Mexico in forested mountains and canyonlands (Gutiérrez et al. 1995, Ward et al. 1995). It is frequently associated with late-successional forests (Ganey and Dick 1995, Gutiérrez et al. 1995) and was listed as threatened in 1993 because of concerns over loss of forested habitat to timber harvest (Cully and Austin 1993). Previous studies (reviewed in Ganey and Dick 1995) suggest that Mexican Spotted Owls are highly selective in terms of roosting and nesting habitat but forage in a wider array of habitats. Consequently, a recovery plan prepared for the Mexican Spotted Owl (Block et al. 1995) explicitly assumed that availability of roosting/nesting habitat was a key factor limiting the distribution of this owl. Thus, understanding factors underlying use of roosting habitat by Mexican Spotted Owls may be critical to managing habitat for this owl.

Several studies have examined roosting habitat used by Mexican Spotted Owls. Rinkevich and Gutiérrez (1996) and Willey (1998) described roosting habitat in the canyon country of southern Utah. Owls in this region were not closely associated with forests and typically roosted on cliffs near the bottoms of narrow rocky canyons with complex architecture. Johnson (1997) also observed owls associated with steep canyons and roosting on cliffs in Colorado, but most of the roosts he located were in trees. Farther south, owls in Arizona and New Mexico were more closely associated with forests and typically roosted in trees (Ganey and Balda 1989, 1994, Fletcher and Hollis 1994, Zwank et al. 1994, Seamans and Gutiérrez 1995, Hodgson 1996, Stacey and Hodgson 1999). Roost trees were typically located in well-shaded areas, often low on canyon slopes or in canyon bottoms, in relatively cool areas. Similar results have been reported for both Northern (*S. o. caurina*, Thomas et al. 1990) and California (*S. o. occidentalis*, Gutiérrez et al. 1992) Spotted Owls. This may be at least partially due to an aversion to high daytime temperatures during

the breeding season (Forsman 1976, Barrows 1981, Ganey et al. 1993, but see Verner et al. 1992).

Several factors limit our understanding of forest roosting habitat of Mexican Spotted Owls. With the exception of Zwank et al. (1994), most information is from the breeding season and does not address potential variation in habitat use between seasons. Most studies have either presented little quantitative information on roost sites (Ganey and Balda 1989), were based on small numbers of owls in limited areas (Ganey and Balda 1994, Zwank et al. 1994, Hodgson 1996, Stacey and Hodgson 1999), or lumped sites from widely-disparate geographic areas or forest types when summarizing roost-site characteristics (Fletcher and Hollis 1994). All of these factors limit our understanding regarding the extent and sources of variability in habitat use by roosting owls.

In conjunction with studies of home-range size and habitat-use patterns of radio-marked Mexican Spotted Owls in Arizona and New Mexico, we sampled habitat characteristics throughout the year at 1790 roost sites. Our objectives were to explore patterns of variation (owls, areas, and seasons) in roost-site characteristics and describe those roost sites by study area and season. In doing so, we hoped to increase understanding of roost-site characteristics in general and of the extent and sources of variability in roost-site characteristics.

STUDY AREAS

We radio-marked Mexican Spotted Owls in three study areas. The Bar-M Canyon study area was located within the Bar-M and Woods Canyon watersheds, Coconino National Forest, approximately 40 km south of Flagstaff, Arizona. The other study areas were selected to represent different habitat situations within the Sacramento Mountains of southcentral New Mexico. The first area (mesic study area) was located along the Rio Peñasco drainage, approximately 12 km southeast of Cloudcroft, New Mexico. The second study area (xeric study area) was located in and around the Sixteen Springs drainage, approximately 18 km northeast of Cloudcroft and approximately 30 km from the mesic study area.

Elevation in the Bar-M Canyon study area ranged from 1850–2440 m. Topography was relatively gentle with rolling terrain broken by scattered volcanic buttes and small

canyons. Most of the study area consisted of ponderosa pine (*Pinus ponderosa*) forest with scattered meadows or parks. Gambel oak (*Quercus gambelii*) was a common associate in forested areas. Alligatorbark juniper (*Juniperus deppeana*) was present in many stands, particularly on warmer, drier sites. Small pockets of quaking aspen (*Populus tremuloides*) also occurred throughout the study area and small numbers of narrowleaf cottonwood (*P. angustifolia*) and box elder (*Acer negundo*) occurred in some canyons.

Topography in the Sacramento Mountains was dominated by moderate to steep montane canyons. Elevation in the mesic study area ranged from approximately 2400–2800 m. Many canyon bottoms consisted of meadows, whereas forests dominated canyon slopes and ridgetops. The predominant forest type was a relatively mesic mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*) and/or white fir (*Abies concolor*). South-western white pine (*P. strobiformis*) was prominent in most stands and ponderosa pine and quaking aspen were frequently present. Elevation in the xeric study area ranged from approximately 2000–2500 m. This study area contained a complex mosaic of mesic and xeric forest types. Mixed-conifer forest was restricted to cool microsites such as drainage bottoms and north-facing slopes. Most south-facing slopes and ridgetops were dominated by woodlands of pinyon pine (*P. edulis*) and alligatorbark juniper, sometimes intermixed with ponderosa pine. Other slopes were dominated by ponderosa pine forest, sometimes with a prominent component of Gambel oak.

METHODS

Field Sampling. We sampled habitat characteristics at 1790 diurnal roost sites used by 28 radio-marked owls (12 females and 16 males). All radio-marked owls were ≥ 1 -yr-old. Roost sites were located by homing in on the radio signal until the owl was observed. If the observer moved slowly, it was often possible to locate the owl and sample habitat characteristics without causing the owl to move. When it appeared that the owl might move, sampling of some variables was omitted to minimize disturbance to the owls. This resulted in missing data, as did human errors (e.g., forgetting to bring sampling equipment). These missing data limited the types of analyses we could conduct, but appeared to be randomly distributed and unrelated to factors in analyses. Further details on capture, radio-marking, and tracking of owls are given in Ganey et al. (1999).

Habitat sampling was essentially plotless, but focused on the roost “microsite,” including the roost tree and its immediate surroundings. The sampling scale represented a tradeoff between our desire to sample characteristics at the actual site used by the owl (rather than simply in a forest stand or general area used by the owl) and our desire to minimize disturbance to roosting owls. Because it was usually possible to sample the microsite quickly, we suspected that sampling at this scale minimized disturbance to radio-marked owls relative to sampling larger plots.

Methods for sampling habitat characteristics largely followed Solis (1983). We estimated percent slope using a clinometer. Two samples were taken per site, one up and one down-slope, then averaged for an overall estimate.

We estimated aspect of the major slope axis using a compass. To estimate percent canopy cover around the roost tree, we used a spherical densiometer to sample canopy cover at a point 5 m from the roost tree in each cardinal direction, then averaged these samples for an overall estimate. Although we use the term canopy cover here, we recognize that the densiometer actually indexes both vertical and horizontal cover, and thus provides a composite measure of both types of cover. For roost trees sampled, we recorded tree species and measured diameter at breast height (dbh) to the nearest cm using a dbh tape. Roost tree and owl perch heights were estimated to the nearest m using a clinometer. We estimated overstory height as the average of the heights of the three overstory trees nearest to the roost tree (sampled with a clinometer). We computed an index of relative roosting height as (owl roost height/roost tree height) $\times 100$.

We also recorded information on forest cover type, roost tree species, and slope position. Cover type assignment was based on a visual assessment of the dominant and co-dominant tree species present. Mixed-conifer forests were dominated by Douglas-fir and/or white fir. Pine-oak forests were dominated by ponderosa pine with Gambel oak co-dominant; pine forests without a prominent oak component were classified as ponderosa pine forest. Forests that did not fit one of the above descriptions were classified as “other.”

Slope position was based on a combination of visual assessment in the field and use of topographic maps. Three categories were recognized: upper third of slopes and ridgetops, middle third of slopes, and lower third of slopes and canyon bottoms.

Data Analysis. Potential sources of variation in roost-site characteristics included individuals, sexes, study areas, and seasons. Because of problems with missing data and diverse variable scales and types, we could not use standard multivariate techniques to partition the variance among these potential sources. Consequently, we explored patterns of variation within study areas by estimating similarity among all possible pairs of roost sites within a study area and summarizing patterns in these similarity estimates using a linear model developed by Dyer (1978). Analyses were conducted within study areas because habitats randomly available varied, sometimes greatly, among study areas.

We used Gower’s (1971) coefficient (S_{ij}) to estimate similarity. This coefficient measures similarity on a scale ranging from 0 (where all characteristics differ between samples) to 1 (where all characteristics are identical between samples). The coefficient handles both quantitative and categorical variables, deals conservatively with missing data, and is not sensitive to differences in the scale at which variables were measured (Gower 1971). Similarity between roost sites i and j over k variables was estimated as:

$$S_{ij} = \sum (s_{ijk}) / \sum (\delta_{ijk}),$$

where s_{ijk} measures similarity between roost sites i and j over variable k , and δ_{ijk} represents the possibility of comparing variable k between roost sites i and j ($\delta_{ijk} = 0$ when data are missing for either or both roost sites, 1 otherwise). Where $\delta_{ijk} = 0$, we set $s_{ijk} = 0$ (Gower 1971).

Ten habitat variables were included in the similarity

estimates. Quantitative variables included percent slope, roost tree dbh, roost tree height, owl perch height, over-story height, canopy cover, and relative owl height. Categorical variables included cover type, position on slope, and roost tree species. For categorical variables, we set $s_{ijk} = 1$ if roost sites i and j agreed for variable k , 0 otherwise (Gower 1971). For continuous variables with values x_1, x_2, \dots, x_n of variable k over n roost sites, we set $s_{ijk} = 1 - [(x_i - x_j)/R_k]$, where R_k is the range of variable k in the sample.

We computed S_{ij} using a Fortran program. We then used a regression model (Dyer 1978) to estimate the effect of two factors (owl and season) on similarity estimates for all possible pairs of roost sites:

$$S_{ij} = \beta_0 + \beta_1 \Delta_{ij}^{\text{owl}} + \beta_2 \Delta_{ij}^{\text{season}},$$

where S_{ij} is the similarity estimate for roost sites i and j , and dummy variable $\Delta_{ij}^{\text{owl}} = 0$ if roost sites i and j were from the same owl and 1 if roost sites i and j were from different owls. Similarly, $\Delta_{ij}^{\text{season}} = 0$ if the two roost sites were from the same season and 1 if not. Sex and territory were not included as factors because they were confounded with owl and because both pair members were radio-marked for only 3 of 11 pairs of owls represented in the Sacramento Mountains. We recognized two seasons, breeding (1 March–30 August) and nonbreeding (1 September–28 February).

Because we sampled multiple roost sites for individual owls, and because a given roost site was included in multiple similarity estimates, there was potentially a high degree of correlation among these estimates (Dyer 1978). To account for this correlation among similarity coefficients estimated between two observations on the same owl, or between two observations on the same pair of owls, we used a repeated-measures model (Morrison 1976, Littell et al. 1996) to estimate regression coefficients. This model estimated a separate within-subject variance and correlation for the same owl or same pair of owls for each season. Degrees of freedom for test statistics on regression coefficients were calculated based on the number of individual owls per study area, rather than on the number of roost sites or pairwise comparisons. This is a conservative approach, similar to a Greenhouse-Geisser maximum reduction in degrees of freedom (Morrison 1976:214), designed to address nonindependence of within-owl samples. We used the likelihood ratio test statistic comparing the model with the correlation structure to the null model without correlation structure to assess the improvement in model fit due to incorporating the correlation structure (Littell et al. 1996). Computations were done using SAS PROC MIXED (v 6.12; SAS Institute Inc. 1997).

We were interested in data on aspect of roost sites because some studies have suggested that roost sites are concentrated on north- or east-facing slopes (Fletcher and Hollis 1994, Seamans and Gutiérrez 1995) and previous evidence suggested that owls may select cool microsites (Barrows 1981, Ganey et al. 1993), which may occur mainly on certain aspects. We did not include data on aspect at roost sites in the above analysis, however, because we were not certain how use of circular data would affect similarity estimates. Instead, we analyzed data on roost-site aspect separately, using Oriana for Win-

dows (version 1.01, Kovach Computing Services, Pentraeth, Anglesey, Wales, U.K.). For each individual owl, we estimated the mean slope aspect (a , hereafter referred to as mean azimuth) and the angular deviation (s) around the mean azimuth by season. We tested the hypothesis that roost sites of individuals within season were not significantly concentrated around the mean azimuth, using Rayleigh's z statistic (Zar 1974). Where this hypothesis was rejected, we tested the hypothesis that mean azimuths of individuals did not differ between seasons using the Watson-Williams test (Zar 1974). This test was conducted separately for each owl.

For each study area and season, we estimated an overall a and s for that study area, using mean azimuths of individual owls as input. We tested the hypothesis that mean azimuths of individuals were not significantly concentrated around the mean azimuth for the study area, using Rayleigh's z statistic. We tested the hypothesis that mean azimuths did not differ between seasons within study area, using the Watson-Williams test.

RESULTS AND DISCUSSION

The repeated-measures model, which assumed that pairs of roost sites compared between the same owl or pair of owls within a season were variably correlated, significantly improved model goodness-of-fit over a null model assuming no correlation ($P < 0.0001$). After accounting for the correlation structure inherent in the data, similarity between roost sites was relatively high in all study areas, ranging from 0.744 in the Sacramento Mountains xeric area to 0.775 in the Bar-M Canyon area. The effects of including a different owl or season in comparisons were slight but detectable in all three areas (Table 1).

Because owls often return to the same stand or general area to roost, especially during the breeding season, similarity estimates could be biased high. Arguing against this explanation, however, is the fact that owl and season effects were relatively slight. That is, comparing roost sites between different owls (which use different portions of a study area) or different seasons decreased similarity only slightly. This suggested that similarity estimates were not biased high by repeated use of the same area by individuals. Rather, it suggested that within a study area, roost sites varied little among owls or between seasons.

The relative magnitude of the effects of owl and season differed among study areas, however. The owl effect was an order of magnitude greater in the mesic area than the season effect. In contrast, this pattern was reversed in the Bar-M Canyon area, and neither effect was pronounced in the xeric area (Table 1). Because at least one study area

Table 1. Regression coefficients for repeated-measures models relating Gower's similarity coefficient between roost sites of radio-marked Mexican Spotted Owls^a to owl identity and season. Separate models were estimated for each of three study areas in Arizona and New Mexico.

EFFECT	SACRAMENTO MOUNTAINS, NEW MEXICO								
	BAR-M CANYON, ARIZONA			MESIC STUDY AREA			XERIC STUDY AREA		
	β	SE	P	β	SE	P	β	SE	P
Intercept	0.775	0.0013	<0.001	0.746	0.0005	<0.001	0.744	0.0008	<0.001
Owl	−0.012	0.0014	<0.001	−0.011	0.0005	<0.001	−0.007	0.0008	<0.001
Season	−0.041	0.0008	<0.001	−0.001	0.0003	0.014	−0.004	0.0006	<0.001

^a Number of owls represented by study area = 13 (Bar-M Canyon), 8 (Sacramento Mountains mesic area), and 7 (Sacramento Mountains xeric area). Number of roost sites sampled = 418 (Bar-M Canyon), 831 (Sacramento Mountains mesic area), and 541 (Sacramento Mountains xeric area). Number of pairwise comparisons = 87,153 (Bar-M Canyon), 344,865 (Sacramento Mountains mesic area), and 146,070 (Sacramento Mountains xeric area).

showed a relatively strong seasonal effect on similarity estimates between roost sites and availability of habitat characteristics varied among study areas, we stratified descriptive statistics for roost-site characteristics by study area and season (Tables 2, 3). Examination of roost-site characteristics provided some possible explanations for the observed differences among areas in similarity estimates. For example, several variables (canopy cover, roost tree species, and slope position) showed more seasonal variation in the Bar-M Canyon area than the other study areas, perhaps explaining the greater seasonal effect observed there. Relative to the breeding season, owls in this area roosted less frequently in Gambel oak during the nonbreeding season, and

roosted more often in the middle third of slopes (Table 3). They also used roost sites with markedly lower canopy cover than those used during the breeding season (Table 2). We suspected that the reduced use of deciduous Gambel oak could be explained by the fact that it loses most of its foliage during most of the nonbreeding season. Thus, it would provide neither hiding nor thermal cover for roosting owls for much of this season. The shedding of oak leaves may also explain the lower canopy cover observed at nonbreeding-season roosts in this study area. Most of these roost sites were in pine-oak forest (Table 3). Canopy cover should have been uniformly lower in this forest type to the extent that oak foliage no longer con-

Table 2. Descriptive characteristics of roost sites of radio-marked Mexican Spotted Owls^a in three study areas in Arizona and New Mexico during the breeding and nonbreeding seasons. Shown are means and standard deviations in parentheses.

VARIABLE	SACRAMENTO MOUNTAINS, NEW MEXICO					
	BAR-M CANYON, ARIZONA		MESIC STUDY AREA		XERIC STUDY AREA	
	BREEDING	NONBREEDING	BREEDING	NONBREEDING	BREEDING	NONBREEDING
Slope (%)	18.9 (13.4)	15.9 (10.8)	35.5 (17.6)	32.6 (16.4)	37.2 (16.0)	29.5 (15.9)
Canopy cover (%)	74.0 (17.0)	59.4 (17.5)	76.0 (13.0)	79.7 (11.8)	69.9 (14.0)	70.3 (20.0)
Roost tree dbh (cm)	32.3 (14.2)	31.1 (11.6)	40.0 (17.1)	42.7 (19.2)	28.5 (13.0)	32.3 (14.6)
Roost tree height (m)	15.2 (7.1)	15.5 (5.5)	20.3 (8.8)	20.9 (7.5)	15.1 (5.8)	16.1 (5.8)
Overstory height (m)	22.3 (5.5)	21.0 (5.7)	29.0 (5.2)	27.3 (5.5)	22.3 (5.2)	20.9 (5.6)
Owl perch height (m)	9.5 (5.2)	10.0 (4.2)	8.2 (4.2)	8.9 (4.0)	6.6 (2.6)	6.9 (3.1)
Relative owl height (%) ^b	64.0 (19.5)	65.8 (18.1)	44.5 (19.6)	45.5 (19.6)	46.0 (16.4)	44.1 (16.7)

^a Number of owls represented by study area = 13 (Bar-M Canyon), 8 (Sacramento Mountains mesic area), and 7 (Sacramento Mountains xeric area). Number of roost sites sampled for breeding and nonbreeding seasons = 148 and 270 (Bar-M Canyon), 467 and 364 (Sacramento Mountains mesic area), and 287 and 254 (Sacramento Mountains xeric area). Sample sizes varied for individual variables due to missing data.

^b Relative owl height = (owl height/roost tree height) × 100.

Table 3. Summary statistics (% of sites) for categorical variables at roost sites of radio-marked Mexican Spotted Owls on three study areas in Arizona and New Mexico. Sample sizes (in parentheses) differed by variable, and refer to number of roosts for which variable was recorded.

	SACRAMENTO MOUNTAINS, NEW MEXICO					
	BAR-M CANYON, ARIZONA		MESIC STUDY AREA		XERIC STUDY AREA	
	BREEDING	NONBREEDING	BREEDING	NONBREEDING	BREEDING	NONBREEDING
Cover type	(N = 146)	(N = 262)	(N = 467)	(N = 364)	(N = 287)	(N = 254)
Mixed-conifer			97.4	96.4	90.7	82.4
Ponderosa pine	0.7	3.1			2.7	6.1
Pine-oak	99.3	96.9				
Other			2.6	3.6	6.6	11.5
Slope position	(N = 131)	(N = 268)	(N = 467)	(N = 364)	(N = 287)	(N = 254)
Upper third/ridgetop	43.5	36.6	13.7	19.2	17.4	17.9
Middle third	24.4	40.3	28.7	22.5	22.8	17.6
Lower third/canyon bottom	32.1	23.1	57.6	58.2	59.8	64.5
Tree species	(N = 148)	(N = 270)	(N = 462)	(N = 361)	(N = 287)	(N = 254)
Ponderosa pine	63.5	91.1	2.6	4.7	12.8	17.4
Gambel oak	36.5	8.9	14.7	6.6	11.6	8.5
Douglas-fir			32.5	42.7	55.8	53.0
White fir			35.1	33.8	7.3	4.4
Southwestern white pine			10.8	8.6	9.5	13.0
Other			4.3	3.6	3.0	3.7

tributed to overall canopy cover. There did not appear to be a clear ecological reason for the seasonal variation in slope position, unless increased use of mid-slope positions provided thermal advantages. Possible examples here included avoidance of lower temperatures in canyon bottoms, avoidance of higher winds along upper slopes, or owls seeking greater solar insolation (i.e., basking) during cold weather.

Despite the variability among study areas, however, some consistent trends were apparent. For example, owls in all three study areas generally roosted in the middle third of mid-sized trees (\bar{x} dbh = 28.5–40.0 cm; Table 2) that were surrounded by taller trees. Canopy cover at roost sites averaged between 70–80% except for during the nonbreeding season in the Bar-M Canyon study area. With the exception of three variables related to tree size, roost site characteristics appeared quite similar between the two Sacramento Mountains study areas (Tables 2, 3). We suspected that this was largely because, although the areas differed in overall habitat composition, owls in both areas roosted primarily in mixed-conifer forest. Interestingly, those variables related to tree size (roost tree dbh, roost

tree height, and overstory height) were more similar between the Bar-M Canyon and Sacramento Mountains xeric areas than between either of those areas and the Sacramento Mountains mesic area (Table 2), possibly indicating convergence in tree use between the two drier study areas.

Slope aspect at roost sites was significantly ($P < 0.05$) concentrated around the mean azimuth for all owls during both seasons in both study areas in the Sacramento Mountains, and for all owls during the breeding season in the Bar-M study area. In contrast, four of 13 owls tested during the nonbreeding season in Bar-M showed no significant orientation. Mean azimuth differed between seasons for two of six owls tested in the mesic study area, two of six in the xeric study area, and six of eight in the Bar-M study area.

Mean azimuths for individual owls were significantly concentrated ($P < 0.05$) around the mean azimuth for each study area and season except for the Bar-M area during the nonbreeding season (Table 4). Mean azimuth differed between seasons in the Bar-M study area ($F_{1,19} = 8.60, P = 0.009$), but not in the mesic ($F_{1,12} = 0.729, P = 0.41$) or xeric areas ($F_{1,12} = 0.009, P = 0.98$). In general,

Table 4. Summary statistics for orientation of roost sites of radio-marked Mexican Spotted Owls in Arizona and New Mexico by study area and season. Statistics based on mean azimuths for roost sites of individual owls within study areas. *N* = number of owls.

AREA	<i>N</i>	BREEDING SEASON				<i>N</i>	NONBREEDING SEASON			
		<i>a</i> ^a	<i>r</i> ^b	<i>s</i> ^c	<i>P</i> ^d		<i>a</i> ^a	<i>r</i> ^b	<i>s</i> ^c	<i>p</i> ^d
Mesic	7	84.7	0.72	46.7	0.021	7	105.6	0.77	41.5	0.010
Xeric	6	28.2	0.95	17.5	<0.001	6	28.7	0.93	22.2	0.002
Bar-M	8	318.8	0.78	40.2	0.004	13	236.6	0.47	70.3	0.053

^a *a* = mean azimuth (°).
^b *r* = length of mean vector.
^c *s* = circular standard deviation.
^d *P*-values based on Rayleigh's *z* statistic.

roosts were oriented toward the east in the mesic area and the northeast in the xeric area during both seasons, with a slight shift to the south evident during the nonbreeding season in the mesic area. Roost sites in the Bar-M area were generally oriented toward the northwest during the breeding season and the southwest during the nonbreeding season. Thus, mean aspects were generally similar between seasons in mixed-conifer forest, but shifted to the south in pine-oak forest during the nonbreeding season. Seasonal differences in roost microclimate would thus likely be greatest in the Bar-M Canyon area, where owls not only roosted more on southerly aspects, but also in more open-canopied situations (Table 2) where they could receive more solar insolation.

CONCLUSIONS

Our results suggested that, at the scale sampled, roost-site characteristics were similar both within and among owls within a study area. They further suggested that microsite characteristics were similar between seasons within two study areas where owls roosted primarily in mixed-conifer forest (Sacramento Mountains), but differed more between seasons within a study area where owls roosted primarily in pine-oak forest (Bar-M Canyon). This suggested that mixed-conifer forest provides stable and favorable conditions for owls year-round, whereas owls residing in pine-oak forests are forced to make greater seasonal adjustments in roost-site use. Finally, our results also suggested that microsite characteristics differed among study areas, as might be expected given differences in habitat availability.

Most previous data on roosting habitat of Mexican Spotted Owls has been specific to breeding-

season roost sites, and our results add information collected during the nonbreeding season. Our results generally support analyses at coarser spatial scales suggesting that Mexican Spotted Owls roost primarily in mixed-conifer or pine-oak forests with high canopy cover (Ganey and Balda 1989, 1994, Fletcher and Hollis 1994, Zwank et al. 1994, Ganey and Dick 1995, Seamans and Gutiérrez 1995, Hodgson 1996, Ganey et al. 1999). We suspected that the differences observed in use of cover types among areas was attributable to climatic differences and local occurrence of those cover types that provided the types of well-structured, closed-canopied stands favored by Mexican Spotted Owls (e.g., Ganey and Dick 1995, Seamans and Gutiérrez 1995, Grubb et al. 1997).

Results from the Sacramento Mountains study areas also generally agreed with existing results suggesting that owls roost primarily on the lower portions of relatively steep, north- or east-facing slopes (Fletcher and Hollis 1994, Seamans and Gutiérrez 1995). In contrast, owls in the Bar-M study area tended to roost more often on moderate slopes, on west-facing slopes, and on middle and upper portions of slopes. We suspected that this reflected the importance of the oak component to stand structure in the Bar-M Canyon study area. Because Gambel oak can thrive in more open, sunny, and warm conditions (Moir 1993), well-structured stands may develop on more exposed upper slopes in this study area. This suggested that owls seek out appropriate habitat where it exists, that such habitat is not always restricted to steep slopes, canyon bottoms, or north- or east-facing slopes, and that development of well-structured habitat may occur in different locales in different forest

types. This in turn suggested that, where management of Mexican Spotted Owl habitat is an objective, land managers should incorporate knowledge of stand-development patterns in different forest types and topographic locations in planning decisions (see also Camp et al. 1997). Finally, managers may also need to consider seasonal patterns in roost-site selection where owls roost in pine-oak forest. Providing conditions suitable for breeding-season roosts, for example, may not adequately provide for the owls' needs during the nonbreeding season.

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BARRED OWL AND SPOTTED OWL POPULATIONS AND HABITAT IN THE CENTRAL CASCADE RANGE OF WASHINGTON

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ABSTRACT.—The Barred Owl (*Strix varia*) has continued to expand its range southward into the northwestern United States from Canada since the 1970s, and has become an established member of the forest avifauna in western Washington. There is increasing concern that it may be competing for resources with the threatened Northern Spotted Owl (*S. occidentalis caurina*) throughout its range. We surveyed for Spotted Owls over an extensive area of the central Cascade Range of Washington during the breeding seasons of 1991–93. Both Spotted Owls and Barred Owls responded to tape recordings and vocal imitations of Spotted Owl calls. By using pair responses or grouping single owl responses from close geographic locations on at least three different survey nights, site centers representing probable breeding pairs or territorial single individuals were designated for both species. A total of 53 Barred Owl and 62 Spotted Owl site centers were identified in the 1280 km² survey area. Barred Owls were found at greatest densities on the wetter, western portions of the Cascade Range. On the driest, eastern portions of this mountain range, Barred Owls were usually found along major river and stream corridors, in the vicinity of forested wetlands, or at higher elevations receiving increased precipitation. We compared the extent of mature, young, and other forest habitats at radii of 0.8 and 1.6 km around site centers of both species. Spotted Owls used sites with greater amounts of mature coniferous forest than did Barred Owls within 0.8 km of site centers across all portions of the study area. Additionally, we found no evidence of mixed-species pairing or hybrids of the two species during the study, suggesting that extensive hybridization may not be occurring where Barred Owls have become firmly established within the range of the Spotted Owl.

KEY WORDS: *Barred Owl*; *Strix varia*; *Northern Spotted Owl*; *Strix occidentalis*; *interbreeding*; *populations*; *habitat*; *Washington*.

Poblaciones y habitat de *Strix varia* y *Strix occidentalis* en el central Cascade de Washington

RESÚMEN.—*Strix varia* ha continuado expandiendo su rango hacia el sur dentro del noroeste de los Estados Unidos desde Canada a partir de 1970. Allí se ha establecido como miembro de la avifauna de bosque en el oeste de Washington. Existe una creciente preocupación de que pueda estar compitiendo por recursos con el amenazado *Strix occidentalis caurina* a lo largo de su rango. Examinamos una vasta area en busqueda de *Strix occidentalis* en la región del Central Cascade de Washington durante las estaciones reproductivas de 1991–93. Ambos buhos respondieron a las grabaciones e imitación de vocalizaciones de *Strix occidentalis*. Mediante la utilización de respuestas pareadas o la agrupación de respuestas únicas de localidades geográficas cercanas en al menos tres noches diferentes de investigación, fueron encontrados los sitios centrales los cuales probablemente representaron a parejas en reproducción o a individuos territoriales de las dos especies. Un total de 53 sitios centrales de *Strix varia* y 62 sitios centrales de *Strix occidentalis* fueron identificados en los 1280 km² investigados. *Strix varia* fue usualmente encontrado a lo largo de los rios y quebradas, en la vecindad de humedales boscosos o a elevaciones mas altas con mayor precipitación. Comparamos la extensión de bosques maduros y juvenes y otros tipos de habitat boscoso en un radio de 0.8 y 1.6 km alrededor de los sitios de centro de ambas especies. *Strix occidentalis* utilizó sitios con mayor cantidad de bosques de coníferas maduros que *Strix varia* dentro de 0.8 km del sitio de centro a traves de todas las porciones del área de estudio. Adicionalmente, no encontramos evidencia de especies mezcladas en pareja o híbridos de las dos especies durante el estudio sugiriendo que la

hibridación no está ocurriendo en los sitios en los cuales *Strix varia* se ha bien establecido dentro del rango de *Strix occidentalis*.

[Traducción de César Márquez]

The Barred Owl (*Strix varia*) is a relatively recent member of the forest avifauna of Washington state. The species was first reported in the mid-1960s in northeastern Washington. West of there, in the northern Washington Cascades, the first pair was recorded in 1974 (Taylor and Forsman 1976). The Barred Owl began to invade the range of the Northern Spotted Owl (*S. occidentalis caurina*) in southwestern British Columbia by the early 1970s (Dunbar et al. 1991). Barred Owls have apparently become more numerous than Spotted Owls over a short period of time at the northern edge of the Northern Spotted Owl's range. From 1985–88, for example, extensive surveys in southwestern British Columbia found 57 Barred Owl territories and 14 Spotted Owl territories (Dunbar et al. 1991). Similarly, in 1985, Hamer (1988) found 15 Barred Owl territories and 8 Spotted Owl territories in northwestern Washington. By the 1990s, Barred Owls had expanded their range through Oregon and become established in northern California in the southern reaches of the Northern Spotted Owl's range (Dark et al. 1998).

Both Barred Owls and Spotted Owls are similar in size, select mature forest habitats (Gutiérrez et al. 1995, Haney 1997, Mazur et al. 1997), and appear to have some overlap in prey use (Devereaux and Mosher 1984, Gutiérrez et al. 1995). Possible competition between the two species may favor the slightly larger and possibly more aggressive Barred Owl (Sharp 1989, Hamer et al. 1994, Dark et al. 1998). The Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl (Thomas et al. 1990) noted that potential competition with the Barred Owl was of immediate concern in maintaining viable Spotted Owl populations in the northern Cascades of Washington (north of Mount Rainier). Considering the rapid spread of this congener across the range of the Northern Spotted Owl, understanding the habitat relationships of the two species in areas where they are now sympatric is important for future conservation planning for this threatened owl.

During extensive surveys for Spotted Owls, we noted that Barred Owls responded regularly to broadcasts of tape recordings and vocal imitations of Spotted Owl calls (see also Dunbar et al. 1991).

We present the results of survey efforts over a 3-yr period, showing relative populations of Barred Owls and Spotted Owls within the area of complete survey coverage. We also investigated whether habitat conditions around territory centers for the two species differed. We hypothesized that mature coniferous forest habitat, known to be important to Spotted Owls, would be used to a greater extent by this species than by Barred Owls.

STUDY AREA AND METHODS

Following listing of the Northern Spotted Owl as a Threatened Species in July 1990, extensive survey programs were initiated to provide site-specific data for the review of timber harvest applications in Spotted Owl habitat. These surveys helped to determine local abundance and distribution of Northern Spotted Owls, particularly in managed forests. We conducted surveys over an extensive and relatively contiguous region of the central Washington Cascades in an area of checkerboard land ownership. The area is typified by alternating sections (16 km²) of public and private ownership. Public lands are administered by the U.S. Forest Service (USFS) and, to a lesser extent, by the Washington Department of Natural Resources (DNR). Surveys were inclusive of all ownerships within the survey boundaries.

The area of survey coverage straddled the crest of the Cascade Mountains in central Washington, extending across both the east and west slopes of the range (Fig. 1). This area included major portions of the upper Green and Yakima Rivers and their tributaries, and minor portions of the upper White and Naches River basins. Topography consisted of steep, mountainous terrain deeply bisected by rivers and streams. Elevations ranged from 400–2000 m and weather ranged from rainy, mild winters with cool summers west of the crest to snowy, cold winters with warm summers east of the crest. The study area was predominantly composed of coniferous forest habitats ranging from early to late successional, with a history of timber harvest and fire disturbance on both private and federal lands. Minor portions of the study area were covered by deciduous or mixed forests (primarily in major river valleys), shrub, herb, and grass-dominated habitats, or bare rock and talus.

The rain-shadow effect of the Cascade Range produces a gradient of forest types from west to east, with moist conifer forests occurring west of the crest, and extending east of the crest for variable distances depending on elevation (higher elevations received more precipitation), this type is gradually replaced by dry conifer forests several kilometers east of the crest. We surveyed for owls in nearly all forested habitats up to 1525 m in elevation. Near this elevation, west of the Cascade crest, low-elevation forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) are replaced by stands of Pacific silver fir (*Abies amabilis*), mountain

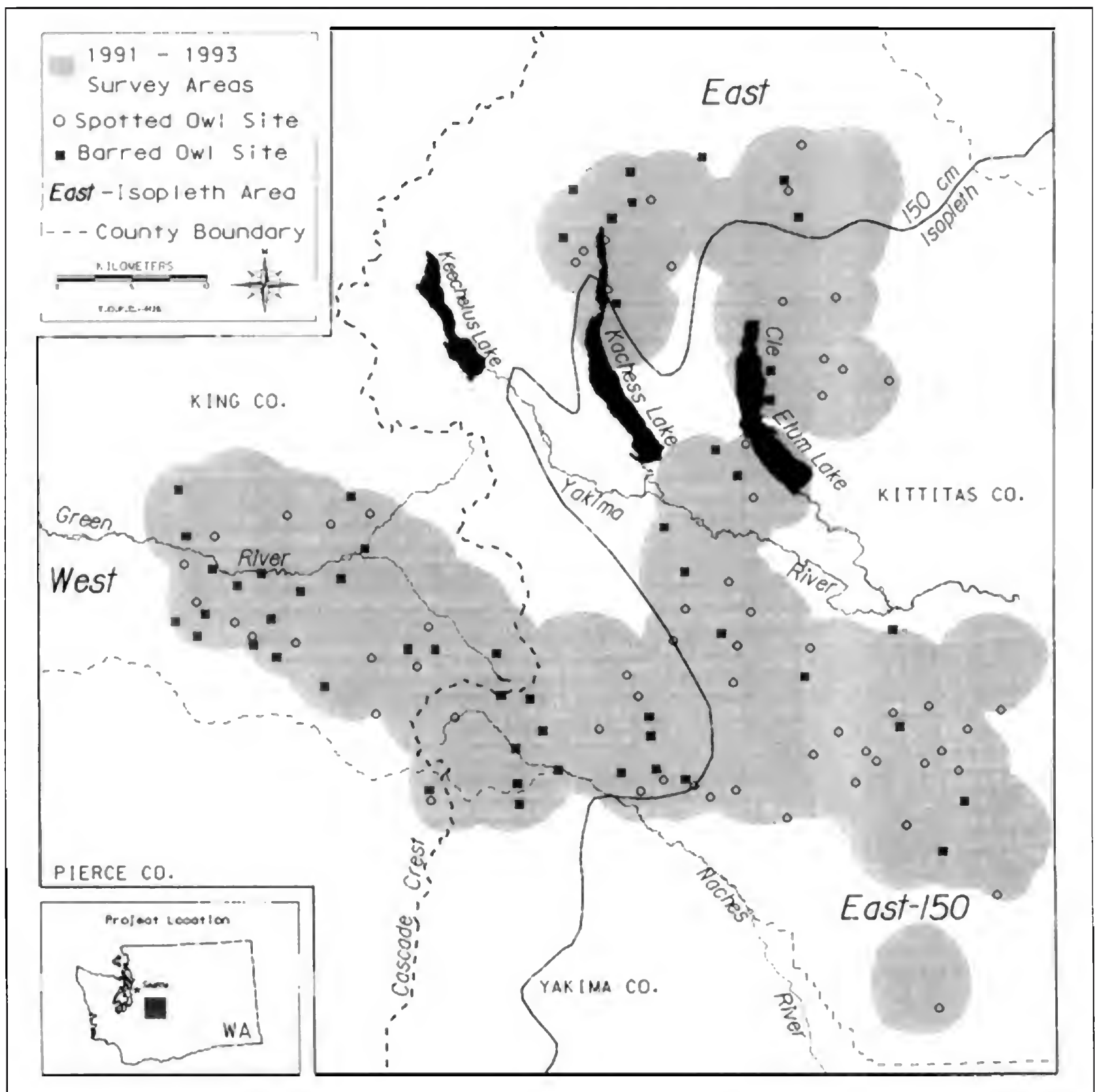


Figure 1. Location of the surveyed area in central Washington showing distribution of Barred Owl and Spotted Owl site centers. The three major subdivisions of the study area based on geography (Cascade crest) and rainfall (150 cm annual isopleth) are also shown.

hemlock (*T. mertensiana*), and noble fir (*A. procera*) at higher elevations. Similarly, low-elevation forests dominated by Douglas-fir, grand fir (*A. grandis*), and Ponderosa pine (*Pinus ponderosa*) in the eastern Cascades are replaced by stands of Pacific silver fir, subalpine fir (*A. lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) at higher elevations. Spotted Owls were not thought to nest above approximately 1525 m in the Washington Cascades (see Allen et al. 1989).

We conducted Spotted Owl surveys from 1991–93, surveying between 15 March–31 August in each year. The

survey season approximated the breeding season for *Strix* owls in the local area. Surveys for Spotted Owls followed U.S. Fish and Wildlife Service (1991, 1992) guidelines for surveying lands proposed for forest management activities. Individual survey areas were established around proposed timber harvest units, extending 2.9 km in radius from the perimeter of each unit (harvest units were 5–35 ha in size). These bounds were selected because a circle of radius 2.9 km (26.4 km²) approximated the average size of a Spotted Owl territory based on regional home range studies (WSFPB 1996). Survey areas often

overlapped, yielding several large regions of complete coverage with rounded perimeters (Fig. 1).

In each survey area, calling stations were established along roads, trails, or on off-trail routes to provide complete audio coverage of all potential habitat of Spotted Owls. Calling stations were typically 0.4–0.8 km apart along roads or trails, with closer spacing in off-trail areas. Surveys consisted of an observer conducting a 10-min visit to each calling station, repeated six times over a survey season, or three times in each of two consecutive survey seasons. All road and most trail stations were visited during hours of darkness, and for safety reasons, some trail and all off-trail stations were visited during the day, usually during afternoon or early evening hours when we suspected owls to be more responsive. During each 10-min calling session, observers imitated calls of Spotted Owls vocally, broadcast a playback of several types of Spotted Owl calls, or used both methods to elicit responses from owls. Calling was interspersed with periods of listening at the observer's discretion, with generally 3–4 min of calls and 6–7 min of listening at each station. Calling was often concentrated at the beginning of the 10-min period, and listening concentrated during the latter half of the 10-min period. Responses from all large owl species were mapped and information on species, sex, movements, and other observations were recorded. All Spotted Owl responses were investigated the following day or as soon as possible to determine reproductive status.

Maps containing Spotted Owl and/or Barred Owl responses from the six survey visits were reviewed following the third and final survey season. Sites where we obtained at least one response from a pair of owls, or at least three responses on three different nights (separated by >7 d) from single owls of either sex within a 0.2-km radius area, were designated as site centers for that species. If an actual nest tree was located, this location then became the site center. The techniques we used to designate site centers for both owl species were essentially identical to procedures used to determine regulatory Spotted Owl site centers by state and federal agencies. Each site center is considered likely to represent a territorial individual or pair (U.S. Fish and Wildlife Service 1992). Previously-known Spotted Owl site centers which were not occupied during our three survey years were not included in the sample. Although we did not follow-up on night responses to determine nest sites for Barred Owls, designation of site centers was usually apparent based on clusters of responses and consistency of response locations in multiple years. We provided six opportunities for territorial owls to respond to our calls and often over three responses were used to determine a site center. In addition, the mountainous terrain helped delimit responses, which were often located in distinct valleys and separated from a nearby site center by an obvious ridge (thereby out of hearing range of the other pair). Simultaneous or near-simultaneous calls from adjacent pairs or singles of the same sex on a given night also helped delimit one site from the next for each species. The actual center was placed on the earliest record of a pair (or nest for Spotted Owls) during a season, and likewise the earliest record of a single if no pair was ever found. Early season responses were assumed to be closer to a potential nest

site than late season responses, although pair responses always took priority over single responses.

We overlaid isopleths of annual precipitation on study area maps to compare the effects of the east-west moisture gradient across the Cascades on owl distribution. We also plotted site centers on habitat maps digitized from 1:64 000 aerial photography. We used mapping that was originally prepared for Spotted Owl management planning based on Washington DNR habitat definitions in use at the time, and separated all habitats into three types: (1) Old Forest Habitat which was dominated by coniferous trees typically over 100 yr old, >60% canopy cover, one to multiple canopy layers, and at least 40% cover of Douglas-fir; (2) Young Forest Habitat which was dominated by trees typically <100 yr old (but of sufficient height and spacing to allow movement of owls during foraging), >60% canopy cover, and typically a single canopy layer; (3) Non-habitat which was made up of forested habitats with overstory trees <10 m in height, stands with <60% canopy cover and/or <40% cover of Douglas-fir, deciduous stands or mixed stands with >25% deciduous overstory, and all forests >1525 m elevation. Shrub, herb and grass-dominated habitats, bare rock and talus slopes, farmland, and water were also included in the Non-habitat category.

To compare habitats near site centers of both species, we drew concentric circles of 0.8- and 1.6-km radius around each site center. Circular areas around Spotted Owl sites have been used in similar investigations of habitat patterns (Lehmkuhl and Raphael 1993, Meyer et al. 1998, Swindle et al. 1999). Habitat comparisons in our study were restricted to mature and young coniferous forest habitats because of the demonstrated importance of mature forests to Spotted Owls (Thomas et al. 1990) and the suggestion that Barred Owls could use stands of younger forest (Hamer 1988).

We followed recent habitat studies of Spotted Owls (Meyer et al. 1998, Swindle et al. 1999) in selecting the two circular areas for determining the nest-site locations of Spotted Owls. Radii of ≤ 0.8 km have been shown to have significant differences in comparisons of habitat around nest sites and random forest sites (Meyer et al. 1998, Swindle et al. 1999), and differences in the amount of old forest may occur up to 1.6 km (Swindle et al. 1999). We stratified owl sites in our area into three subunits based primarily on precipitation criteria: west of the Cascade Range crest, east of the crest to the 150 cm precipitation isopleth, and east of the 150 cm isopleth. Our comparisons of average amounts of each habitat type within the tested radii were achieved using multiple analysis of variance (MANOVA), following tests for normality and use of the Wilks' lambda (likelihood ratio criterion) to test for significant interaction between variables (SYSTAT version 8.0). We randomly sampled circular areas around site centers, and used mutually exclusive (site centers of both species tested at 0.8-km radius were not used for tests at 1.6-km radius), nonoverlapping areas for both radii.

RESULTS

Population Size and Distribution. Spotted Owl surveys, when combined over three breeding sea-

sons, covered 1280 km². Portions of the surveyed area above 1525 m, or extensive areas classified as nonhabitat were not surveyed. We may have missed some Barred Owls by not surveying in forested habitats containing >75% deciduous trees. Large stands of mixed and deciduous forests comprised <2% of the study area and occurred only in the floodplain of the Green and Yakima Rivers. Likewise, stands of <60% canopy closure were uncommon and small in size, and often occurred adjacent to surveyed stands, therefore receiving limited survey coverage (Fig. 1).

A total of 62 Spotted Owl site centers and 53 Barred Owl site centers were identified. Spotted Owls were well-distributed across the area (0.047, 0.043, and 0.053/km² from west to east by subunit; Fig. 1). Barred Owls were most abundant west of the Cascade crest (0.063/km²), with similar densities (0.063/km²) extending east of the crest only within the 150 cm/yr isopleth for annual precipitation. East of this line, Barred Owl densities dropped to 0.019/km². To the west of our survey area within the Cascade Range, only Barred Owls were located during similar surveys from 1991–93 (L. Young pers. comm.). To the east of our study area, several additional Spotted Owl sites and a few Barred Owl sites have been located across northern Kittitas County almost to the forest/sagebrush steppe interface (S. Sovern and M. Taylor pers. comm.). Also, we have found Barred Owls breeding at sites both lower and higher in elevation than known Spotted Owl nest locations. Barred Owls have completely overlapped the known geographic and altitudinal distribution of Spotted Owls in central Washington.

Habitat Analyses. We found no significant differences in the mean amount of all habitat types between Spotted and Barred Owls within the 1.6 km radius analysis area (Wilks' $\lambda = 0.946$, $P = 0.475$) around site centers. Within the 0.8 km radius surrounding Spotted Owl and Barred Owl sites, however, significant differences in mean habitat amounts were detected (Wilks' $\lambda = 0.725$, $P = 0.003$). Spotted Owl sites contained more old forest close to the site center than Barred Owl sites. Within the three geographic regions we tested, MANOVA results indicated that mean amount of habitat differed significantly within the 0.8 km (Wilks' $\lambda = 0.594$, $P = 0.001$) radius. There was consistently more old forest surrounding Spotted Owl sites than Barred Owl sites in all subunits (Table 1). Barred Owl sites also contained more young

forest than Spotted Owl sites in the far west and far east subunits.

In the dry zone of the eastern Cascades east of the 150-cm isopleth, 8 of 12 Barred Owl site centers were found in moister forest situations, such as those along major river or stream drainages or near lakes or wooded swamps or at higher elevations where the true amount of precipitation may actually have exceeded 150 cm/yr. On both slopes of the Cascade Range, several Barred Owl sites occurred in deciduous and mixed forest stands found exclusively in major river valleys. Forest stands dominated by deciduous trees are not considered important Spotted Owl habitat in Washington (WSFPB 1996). East of the 150-cm isopleth, Spotted Owl sites were typically located in coniferous forests on the sides of slopes and were not found in the habitats described above for Barred Owls. West of the 150-cm isopleth and above major river valleys, however, Spotted Owl sites occurred in very similar situations to those of Barred Owls. We did not find Spotted Owl nests in high-elevation, true fir-dominated forests. Our own observations of Barred Owls, plus those of Wright and Hayward (1998), suggest that this species is also more common in lower elevation mixed conifer forests than in high elevation spruce-fir forests.

DISCUSSION

Population Size and Distribution. The full impact of the Barred Owl range expansion into the Pacific Northwest on resident Spotted Owls probably has yet to be fully realized. We detected almost as many Barred Owls as Spotted Owls, and in some portions of the Washington Cascades, Barred Owls have become more numerous than Spotted Owls. We could have missed some territories of both owl species, particularly Barred Owls; however, we received consistent responses from both species at night and during the day, even though we only broadcast Spotted Owl calls. Responses obtained during the day were typically at closer range than at night. Daytime surveys were designed with closer spacing of calling stations and transects to account for this tendency. Even so, we could have missed some owls, particularly Barred Owls, because of individual variation in response levels to calls of a congener.

All Spotted Owl sites known in the survey area were monitored for occupancy and reproduction annually from 1991–98. Of the 62 known sites, 22 were unoccupied at least temporarily by both

Table 1. Comparison of mean hectares of habitat present within selected radii around Barred Owl and Spotted Owl site centers across three geographic regions in the Central Cascade range of Washington.

RADIUS ^b (km)	WEST ^a			EAST ^a			EAST 150 ^a		
	MEAN	95% CI	N	MEAN	95% CI	N	MEAN	95% CI	N
0.8 km									
Old/Mature Forest									
Barred Owl	57	43	10	81	27	11	55	47	4
Spotted Owl	83	32	8	106	42	4	98	30	13
Young Forest									
Barred Owl	72	34	10	42	29	11	41	41	4
Spotted Owl	51	36	8	5	10	4	40	20	13
Non-habitat ^c									
Barred Owl	73	33	10	79	30	11	106	83	4
Spotted Owl	68	35	8	87	33	4	64	20	13
1.6 km									
Old/Mature Forest									
Barred Owl	173	153	8	430	112	9	304	125	8
Spotted Owl	182	136	5	334	85	9	323	97	15
Young Forest									
Barred Owl	354	178	8	91	98	9	163	94	8
Spotted Owl	420	133	5	117	71	9	178	55	15
Non-habitat									
Barred Owl	403	161	8	442	144	9	545	200	8
Spotted Owl	405	42	5	456	156	9	489	103	15

^a West = west of the Cascade Range crest, East = east of the Cascade Range crest but west of the 150 cm/yr rainfall isopleth, East 150 = east of the 150 cm/yr rainfall isopleth.
^b Area within 0.8 km radius = 201 ha; 1.6 km radius = 804 ha.
^c Non-habitat included non-forest, deciduous-dominated forests, and high-elevation forests.

members of the original pairs. Of these 22 sites, half remained unoccupied through 1998. Of the remaining 11 sites, six were reoccupied by different Spotted Owl pairs or single individuals, while Barred Owls were present at or near five site centers. In most cases, Barred Owls were already present in the vicinity (≤ 0.8 km) prior to the disappearance of the Spotted Owl pairs. In one instance, a newly established pair of Spotted Owls nested within 1 km (and hearing distance) of an established Barred Owl site. Surveys over additional years are needed to determine whether Spotted Owls regularly reoccupy sites in close proximity to Barred Owl territories.

Habitat Analyses. In portions of the western Washington Cascades west of our study area where less old forest remained, Barred Owls have occupied second-growth Douglas-fir/western hemlock stands with remnant large trees and snags which provide nest cavities. Spotted owls have been known to occur in landscapes where young forests predominate (Forsman et al. 1988, Irwin et al.

1991), but they persist at low densities and typically nest in a patch of old forest. In our study area, where relatively large stands (>200 ha) of old forest habitat remained, surrounded by a mosaic of managed and unmanaged fire-regenerated habitat, both Spotted Owls and Barred Owls occupied nesting territories and produced young. Our data suggested that Barred Owls persisted in areas with less old forest than Spotted Owls.

Within conservation areas designed for Spotted Owl habitat protection, management options that consolidate and protect preferred habitat for Spotted Owls in well-spaced, large blocks (>100 ha) may help them compete with Barred Owls in Cascade Range forests. Recent studies by Meyer et al. (1998) and Swindle et al. (1999) have also noted a preference for an unfragmented patch of old forest around Spotted Owl nest sites. This does not mean that Barred Owls cannot successfully occupy areas of extensive cover of old forest. Observations by Wright and Hayward (1998) and our own observations in neighboring wilderness areas and na-

tional parks indicated that territorial Barred Owls can occur in wilderness valleys with extensive cover of old forest.

Some competition for resources likely takes place where the two species are sympatric because of significant overlap in habitat use, prey species, and nest-site preferences. Spotted Owls and Barred Owls were previously sympatric in only one other area in North America, at the southern limit of the ranges of both species in the southern Sierra Madre Occidental of Mexico (Enríquez-Rocha et al. 1993, Howell and Webb 1995). In Mexico, there are two different subspecies and the duration of the sympatry has been longer. In our study area, the northern subspecies of both owls appear to co-exist in very similar habitats in the wet, western Cascades, but they may be exhibiting greater habitat separation in the eastern Cascades. In these dryer forests, the predominance of Spotted Owls in conifer forests at mid-slope (Buchanan et al. 1995), and Barred Owls in forested wetlands, mixed riparian stands, and high elevation moist coniferous forests, mirrored the habitat use of the species over the majority of their respective ranges. Spotted Owls, outside the coastal Pacific Northwest, are primarily found in relatively-dry, western mountains, while Barred Owls occur in more mesic habitats in eastern mixed or deciduous forests and boreal forests.

Barred Owls were already well-established on our study area by the time we began our surveys. We found no mixed-species (Barred Owl/Spotted Owl) pairs or hybrid owls, but hybrids have been reported from Washington and other parts of the Northern Spotted Owl range (Hamer et al. 1994). Widespread hybridization in the central Washington Cascades did not appear to be continuing. As shown in other species (Short 1969, Rohwer 1972), it is likely that once Barred Owls established self-sustaining local populations, individuals of the invading species no longer had trouble finding conspecific mates, minimizing the incidence of mixed-species pairing.

Although this study suggests only minor differences in the amount of old and mature forest habitat surrounding Spotted and Barred Owl site centers based on the broad seral stages used in our analyses, perhaps more detailed habitat use studies would indicate more partitioning. The extent that habitat or niche separation will keep the two species from competing directly for resources should be considered speculative. However, direct com-

petition in some habitats appears likely and may negatively affect Spotted Owl population recovery.

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FOOD HABITS OF BALD EAGLES WINTERING IN NORTHERN ARIZONA

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ABSTRACT.—We used pellets collected from roosts to supplement incidental foraging observations to identify prey species of Bald Eagles (*Haliaeetus leucocephalus*) and to evaluate spatial and temporal trends in their food habits while wintering in northern Arizona between 1994–96. We analyzed 1057 pellets collected from 14 roosts, and identified five mammal and 13 bird species. American Coot (*Fulica americana*, $N = 447$) and elk/deer (*Cervus elaphus*/*Odocoileus hemionus*, $N = 412$) were the most common prey remains we identified and they varied annually and inversely with each other (11–58% for coots and 21–78% for elk/deer). Diving ducks (92%) were more heavily represented in pellets with identifiable bird prey ($N = 701$) than dabblers (1%), although Christmas Bird Counts indicated 64% divers and 36% dabblers in the study area ($N = 18\,202$; $\chi^2 = 46.3$, $df = 1$, $P < 0.01$). Almost all pellets consisted mostly of mammal or bird remains ($N = 366$ and 689 , respectively). The overall ratio of mammal to bird pellets was 59:41, with relative class frequencies varying between years ($\chi^2 = 118.29$, $df = 2$, $P < 0.01$). At roosts <3 km from water ($N = 752$), 90% of the pellets contained birds; whereas, at roosts >3 km from water ($N = 303$), 96% of the pellets contained mammals ($\chi^2 = 698.54$, $df = 1$, $P < 0.01$). In three successive winters of varying weather conditions, wintering eagles foraged primarily on mammals, fish, and waterfowl, respectively; but only mammals and waterfowl were accurately represented in pellets.

KEY WORDS: *Bald Eagle*, *Haliaeetus leucocephalus*; pellets; diet; food habits; winter roosts; winter habitat.

Habitos alimenticios de *Haliaeetus leucocephalus* en Arizona

RESÚMEN.—Utilizamos las egragópilas recolectadas en sitios de perchas para complementar las observaciones de forrajeo e identificar las especies de presas de *Haliaeetus leucocephalus* como también para evaluar las tendencias espaciales, temporales y sus hábitos alimenticios durante su estadía de invierno en Arizona entre 1994–96. Analizamos 1057 egragópilas recolectadas en 14 sitios de perchas, identificamos 5 especies de mamíferos y 13 de aves. *Fulica americana* ($N = 447$) y *Cervus elaphus*/*Odocoileus hemionus* ($N = 412$) fueron los restos de presas más comunes identificados. Estos variaron anualmente e inversamente entre ellos (11–58% para *Fulica americana* y 21–78% para *Cervus elaphus*/*Odocoileus hemionus*). Diving ducks (92%) fueron más representados en las egragópilas como aves presa ($N = 701$) que los Dabblers (1%), aunque los Conteos de Navidad indicaron una representatividad de 64% para Olivers y 36% para Dabblers en el área de estudio ($N = 18\,202$; $\chi^2 = 46.3$, $df = 1$, $P < 0.01$). Casi todas las egragópilas fueron restos de mamíferos o aves ($N = 366$ y 689 respectivamente). La proporción total de egragópilas de mamíferos y aves fue de 59:41, con frecuencias relativas de clase entre años ($\chi^2 = 118.29$, $df = 2$, $P < 0.01$). En los sitios de perchas <3 km del agua ($N = 752$), el 90% de las egragópilas contenían aves, mientras que los sitios de perchas a >3 km del agua ($N = 303$), el 96% de las egragópilas contenían mamíferos ($\chi^2 = 698.54$, $df = 1$, $P < 0.01$). En tres inviernos subsecuentes con variaciones climáticas, las águilas forrajearon principalmente mamíferos, peces, y aves acuáticas respectivamente, pero solo los mamíferos las aves fueron representadas con certeza en las egragópilas.

[Traducción de César Márquez]

Food habits of nesting Bald Eagles (*Haliaeetus leucocephalus*) in Arizona are well-documented (Haywood and Ohmart 1986, Hunt et al. 1992, Grubb 1995), but information on the diet of winter migrants is limited (Grubb and Coffey 1982, Grubb and Kennedy 1982, Brown 1993). As part of a long-term study of wintering Bald Eagles in

northern Arizona (Grubb et al. 1989, Grubb et al. 1994, Grubb 1996), we collected pellets from beneath roost trees during three winters from 1994–96. Typically, pellets effectively supplement direct observations and prey remains in determining local diets (Grubb and Kennedy 1982, Stalmaster and Plettner 1992, Isaacs et al. 1993). Fish and

large mammals, for example, can be underrepresented in pellets, and small mammals overrepresented. However, the overall proportion of birds and mammals in pellet analyses tends to reflect actual diet (Mersmann et al. 1992). In northern Arizona, mid-winter foraging on fish is rare (Grubb and Lopez 1997), and prey remains of waterfowl and large ungulate carrion are often difficult to find. In addition, the relatively-small, ephemeral population of wintering eagles limits foraging observations (Grubb and Kennedy 1982, Grubb et al. 1989). Therefore, to supplement limited, incidental foraging observations, we relied primarily on pellets to identify prey species and to evaluate spatial and temporal trends in the food habits of Bald Eagles wintering in northern Arizona.

STUDY AREA AND METHODS

Our study area was the Coconino National Forest, surrounding the town of Flagstaff, Arizona, in Coconino and Yavapai counties. Habitat is dominated by ponderosa pine (*Pinus ponderosa*) forest transitioning into forests of pinyon pine-juniper (*P. edulis-Juniperus* spp.) at lower elevations (Brown 1982). Elevation ranges between 1524–2439 m in semimountainous terrain. The only permanent water bodies in the vicinity of our study roosts were several small lakes (<1000 ha). Winter weather in northern Arizona varies within and between years with occasional heavy snows (<0.6 m) and cold temperatures (lows exceeding -18°C), interspersed with dry periods of mild temperatures (highs to 10°C) and general loss of snow cover.

We collected pellets during three winters: 1993–94, 1994–95, and 1995–96, referred to hereafter as the winters of 1994, 1995, and 1996, respectively. We used daily minimum low temperatures ($^{\circ}\text{C}$) measured at the Flagstaff airport (National Oceanographic and Atmospheric Administration, on-line data) to contrast winter weather conditions between study years (October through March, 1994–96). We measured the distance from each roost to the nearest permanent water on U.S. Geological Survey, 7.5-min quadrangle maps.

We collected pellets from beneath roost trees in 14 previously-identified night roosts (Grubb et al. 1989, Dargan 1991). Bald Eagle use of winter roosts was highly variable, ranging from one eagle in a single tree to >40 eagles in >25 trees. Pellets were collected by walking around roost trees clockwise then counter-clockwise, 2- and 5-m away from the base of the tree, or farther if necessary to accommodate tree lean. We removed pellets from each roost prior to the next field season. We were unable to collect pellets from every 1994 roost during the following two winters because of weather and scheduling limitations. Because 42% of all the pellets collected, and 68% of the 1996 pellets resulted from an exceptional concentration of >40 eagles foraging on waterfowl and using a single roost (hereafter referred to as Roost 8) in 1996, we evaluated annual variation and calculated over-

all class composition with and without data from this roost.

We dissected pellets in the laboratory to determine their contents. Identification of prey items was made to the lowest taxonomic level possible by comparison to avian study skins and mammalian hair samples. Visual estimates of percent volume were made for each taxon. Pellets comprised of >50% mammal or >50% bird remains by volume were classified by predominant class to facilitate comparisons between years, roosts, and habitat. Adorjan and Kolenosky (1969) and Moore et al. (1974) facilitated hair identification, but we could not differentiate elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) hair. However, based on our field observations of available large ungulate carrion, we estimated elk comprised >85% of the elk/deer hair sample. Similarly, Redhead (*Aythya americana*) and Canvasback (*A. valisineria*) feathers in pellets could not be differentiated. Because Redheads greatly outnumbered Canvasbacks on local lakes (Morrall and Coons 1996; National Audubon Society Christmas Bird Counts 1994–96, Laboratory of Ornithology, Cornell University, on-line data; pers. obs.), we estimated they comprised >80% of this feather sample.

We used SPSS 7.5 for Windows (SPSS 1997) to calculate frequencies and descriptive statistics, and chi-square tests for evaluating variation in frequencies of mammal and bird pellets among years and between lake and upland roosts. Sample sizes and percentages are not always additive because some pellets contained more than one class or species. We used the frequency of occurrence (i.e., the number or percent of pellets containing a class or species) as the measure of relative abundance.

RESULTS

We collected 1057 Bald Eagle pellets (Table 1). Of the 885 pellets with distinguishable prey species, 823 (93%) contained only a single species, but 61 (7%) had two species and one (<1%) had three species. We identified five mammal and 13 waterfowl species (Table 2). American Coot (*Fulica americana*, $N = 447$) and elk/deer ($N = 412$) were the most common prey items. Relative frequencies of these two species varied annually and inversely with each other (11–58% for coots and 21–78% for elk/deer). Diving ducks were more heavily represented (92%, including American Coots) than dabblers (1%) in eagle pellets with identifiable avian prey ($N = 701$). However, National Audubon Society Christmas Bird Counts for northern Arizona between 1994–96 (Laboratory of Ornithology, Cornell University, on-line data), indicated much less difference in the numbers of divers (64%) and dabblers (36%) during our study ($N = 18\,202$; $\chi^2 = 46.3$, $\text{df} = 1$, $P < 0.01$). Nine of 12 locally-common species of divers (75%) were identified in our pellet analysis, and four of seven dabblers (57%).

Based on the most prevalent prey species in pellets, we identified 366 mammal, 689 bird, and 2

Table 1. Number of pellets collected each year and the relative frequency (% total number) of mammalian and avian prey by roost and by year, for 1057 pellets collected beneath 14 winter Bald Eagle roosts in northern Arizona, 1994–96.

ROOST (TREES)	DISTANCE TO WATER (km) ^a	NO. PELLETS (% MAMMAL/% BIRD)			
		1994	1995	1996	TOTAL
1 (4)	0.05	2 ^b (50/0)	1 (0/100)	1 (0/100)	4 ^b (25/50)
2 (19)	0.25	30 (13/87)	0	6 (0/100)	36 (11/89)
3 (14)	0.4	51 (69/31)	15 (40/60)	29 (41/59)	95 (56/44)
4 (9)	0.5	22 (0/100)	0	0	22 (0/100)
5 (13)	0.85	14 (7/93)	5 (0/100)	23 (9/91)	42 (7/93)
6 (6)	1.7	2 (0/100)	—	—	2 (0/100)
7 (18)	1.9	0	0	98 (2/98)	98 (2/98)
8 (27)	2.2	5 (60/40)	—	449 (2/98)	454 (3/97)
9 (1)	3.5	1 (100/0)	—	—	1 (100/0)
10 (27)	5.0	38 (100/0)	19 (100/0)	4 (100/0)	61 (100/0)
11 (5)	6.5	12 (100/0)	—	0	12 (100/0)
12 (3)	7.6	1 (100/0)	—	—	1 (100/0)
13 (2)	13.0	12 (100/0)	—	—	12 (100/0)
14 (31)	18.2	110 (91/9)	61 (97/3)	46 ^b (96/2)	217 (94/6)
Totals:					
14 ^c (179)	8L/6U	300 (69/30)	101 (83/17)	656 (11/89)	1057 (35/65)
Totals without Roost 8 ^d					
13 ^c (152)	7L/6U	295 (69/30)	101 (83/17)	207 (31/69)	603 (59/41)

^a Roosts <3.0 km (\bar{x} = 1.0, SD = 0.8) from permanent lakes were classified as lake (L), and roosts >3.0 km (\bar{x} = 9.0, SD = 5.1) were classified as upland (U).
^b One pellet was entirely fish remains.
^c Total number of roosts.
^d Since 42% of all the pellets collected, and 68% of the 1996 sample, came from an unusual concentration of >40 eagles foraging on waterfowl and using Roost 8 in 1996, both typical annual variation and overall class composition were more accurately represented without Roost 8 data.

fish pellets. The overall ratio of mammal to bird pellets, excluding Roost 8, was 59:41, with relative class frequencies varying between years (χ^2 = 118.3, df = 2, P < 0.01). The overall ratio with Roost 8 included was 35:65. Class frequencies were generally consistent at individual roosts from year to year; only Roosts 3 and 8 varied among years (Table 1). However, class frequencies varied between roosts and appeared related to roost distance from permanent water. At roosts <3 km from water (classified as lake roosts), 90% of the pellets contained mostly bird remains (N = 752), whereas at roosts >3 km from water (classified as upland roosts), 96% of the pellets contained mammalian remains (N = 303, χ^2 = 698.5, df = 1, P < 0.01). Conversely, 98% of all bird pellets occurred in lake roosts and 79% of all mammal pellets occurred in upland roosts.

Weather conditions varied among the three

years of our study. Temperatures generally declined from October through mid-December with repeated, brief cold cycles throughout the winter of 1994. During the winter of 1995, generally cold temperatures in November and early December with shorter warming periods than the previous year led to a freeze-over of local lakes by late December. January also had nearly two weeks of unseasonable cold before temperatures began to increase through March. The winter of 1996 was generally mild and characterized by only three, 10–14 d cold cycles between mid-December and late February.

In the relatively-typical winter of 1994, pellets confirmed that Bald Eagles fed primarily on large mammal carrion (69%, Table 1). In 1995, waterfowl numbers were again minimal after freeze-over and, although the number of pellets was down, dependence on mammalian carrion was evident

Table 2. Relative class and species abundance in 1057 pellets collected beneath 14 Bald Eagle winter roosts in northern Arizona, 1994–96.

CLASS/SPECIES	NO. PELLETS (% ANNUAL TOTAL ^a)			
	1994 (N = 300)	1995 (N = 101)	1996 (N = 656)	TOTAL (N = 1057)
Mammal	217 (72)	86 (85)	146 (22)	449 (42)
Elk/mule deer ^b (<i>Cervus elaphus</i> / <i>Odocoileus hemionus</i>)	198 (66)	78 (78)	136 (21)	412 (39)
Cottontail rabbit (<i>Sylvilagus</i> spp.)	27 (9)	4 (4)	6 (1)	37 (4)
Black-tailed jackrabbit (<i>Lepus californicus</i>)	3 (1)	2 (2)	0	5 (<1)
Coyote (<i>Canis latrans</i>)	2 (1)	1 (1)	0	3 (<1)
Unknown mammal	27 (9)	11 (11)	21 (3)	59 (6)
Bird	96 (32)	17 (17)	588 (90)	701 (66)
American Coot (<i>Fulica americana</i>)	59 (20)	11 (11)	377 (58)	447 (42)
Ruddy Duck (<i>Oxyura jamaicensis</i>)	11 (4)	0	93 (14)	104 (10)
Ring-necked Duck (<i>Aythya collaris</i>)	7 (2)	0	26 (4)	33 (3)
Redhead/Canvasback ^b (<i>Aythya americana</i> / <i>Aythya valisineria</i>)	6 (2)	1 (1)	23 (4)	30 (3)
Northern Shoveler (<i>Anas clypeata</i>)	1 (<1)	0	1 (<1)	2 (<1)
Mallard (<i>Anas platyrhynchos</i>)	4 (1)	0	0	4 (<1)
Northern Pintail (<i>Anas acuta</i>)	0	0	1 (<1)	1 (<1)
Green-winged Teal (<i>Anas crecca</i>)	0	0	1 (<1)	1 (<1)
Lesser Scaup (<i>Aythya affinis</i>)	0	0	1 (<1)	1 (<1)
Western Grebe (<i>Aechmophorus occidentalis</i>)	11 (4)	5 (5)	6 (1)	22 (2)
Pied-billed Grebe (<i>Podilymbus podiceps</i>)	1 (<1)	0	4 (<1)	5 (<1)
Eared Grebe (<i>Podiceps nigricollis</i>)	0	0	3 (<1)	3 (<1)
Unknown bird	10 (3)	4 (4)	275 (42)	289 (27)
Unknown fish	1 (<1)	0	2 (<1)	3 (<1)
Other material ^c	6 (2)	3 (3)	27 (4)	36 (3)

^a Numbers and percentages of pellets are not additive because some pellets contained >1 class or species.
^b Species were grouped because hair or feathers present in pellets were not distinguishable.
^c Vegetation, seeds, soil, sand, small stones; monofilament line was also found in one pellet.

(83%). However, the harsh weather conditions caused an extensive die-off of feral fathead minnows (*Pimephales promelas*) which became the primary food we observed Bald Eagles eating that winter (Grubb and Lopez 1997). During 1996, waterfowl remained locally abundant all winter, with large flocks of several hundred birds concentrated in small openings in lake ice during cold periods. Very few road- or winter-killed elk were

observed and pellets confirmed our observations that Bald Eagles fed primarily on birds (89%).

DISCUSSION

The 59:41 frequency ratio of mammal to bird pellets, excluding Roost 8, was consistent with our combined local field experience over the past 24 yr. Bald Eagles wintering in northern Arizona typically depend on elk carrion as their primary food,

beginning in late fall when visceral piles left during hunting season are abundant. Waterfowl provide an opportunistic, alternative food source when available. In similar habitat around Navajo Lake in northern New Mexico, pellets indicated Bald Eagle use of deer and elk carrion varied inversely with small mammal and waterfowl consumption, depending on weather and prey availability (Grubb 1984). Mild weather permits waterfowl to remain on northern Arizona lakes, whereas harsher winter conditions force them to leave and large ungulates to become more vulnerable to road- and winter-kill. Therefore, there is a weather-driven, relatively-stable food base for visiting, winter eagles even though prey classes vary (Grubb and Kennedy 1982). The 35:65 overall ratio of mammal to bird pellets we obtained by including Roost 8 was more representative of a mild winter with abundant-waterfowl, such as in 1996.

Differential foraging by wintering Bald Eagles on diving and not dabbling waterfowl may be a function of winter icing conditions and differing response behaviors to hunting eagles. Since dabbling ducks can launch into flight quickly, they are vulnerable for only a brief period. Divers, on the other hand, require a stretch of open water to get airborne, increasing their exposure to eagle predation. Diving to escape can also leave them vulnerable to foraging Bald Eagles. We have observed eagles circling overhead, singly (Brattstrom 1989) and in cooperative groups (Sherrod et al. 1976), to repeatedly drive their prey back underwater until exhausted. Icing of lake surfaces exacerbates diving duck vulnerability by concentrating large numbers of waterfowl in small areas, precluding flight by reducing take-off space, and limiting the diving area for underwater maneuvering.

In the three successive winters of our study, different weather conditions resulted in Bald Eagles foraging primarily on mammals, fish, and waterfowl, respectively. However, only the 1994 dependence on mammals and 1996 dependence on waterfowl were accurately represented by pellets. Nonetheless, our results suggest that pellets can provide effective assessments of long-term trends in mammal and bird use, and an indication of the relative abundance of prey within each class (Mersmann et al. 1992, Stalmaster and Plettner 1992). Pellet analyses need not be avoided in winter diet assessment (Stalmaster and Plettner 1992), especially under limiting circumstances such as those that we encountered. As demonstrated by our win-

ter 1995 results, pellet analyses should be substantiated with observations as much possible, and the general absence of fish representation should be taken into account. In addition, the variation we recorded in wintering Bald Eagle diet, both annually and among roost locations, mandates a large pellet sample well-distributed over time and space.

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NEST FEATURES AND NEST-TREE CHARACTERISTICS OF SHORT-TOED EAGLES (*CIRCAETUS GALLICUS*) IN THE DADIA-LEFKIMI-SOUFLI FOREST, NORTHEASTERN GREECE

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ABSTRACT.—Data on nest features and nest-tree characteristics of 29 nest trees of Short-toed Eagles (*Circaetus gallicus*) were compared with the same number of paired, randomly-selected trees in the Dadia-Lefkimi-Soufli forest complex, northeastern Greece. Short-toed Eagles usually nested in Calabrian pine (*Pinus brutia*, 83%) trees that were either dominant (87%) or intermediate (13%) in the canopy. Most nests were in the largest trees in terms of height ($\bar{x} = 13.8 \pm 0.4$ m, \pm SE) and diameter at breast height ($\bar{x} = 49.7 \pm 1.6$ cm) in stands. Nests were located in the lower or middle third of the canopy at a mean height of 8.6 ± 0.41 m and on horizontal branches at a mean distance of 133 ± 12.4 cm from trunks. A tendency for building nests on the south-facing side of canopies of nest trees was detected (mean angle = 178° , angular deviation $s = 58^\circ$). Short-toed Eagles selected nest trees that provided them with easy access while also providing protection from predators and inclement weather.

KEY WORDS: *Short-toed Eagle*, *Circaetus gallicus*; nest features; nest-tree characteristics; Greece.

Características del nido y de los árboles con nido de *Circaetus gallicus* en el bosque Dadia-Lefkimi-Soufli en el noreste de Grecia

RESÚMEN.—Comparamos los datos sobre las características de 29 nidos de *Circaetus gallicus* con el mismo número de árboles seleccionados al azar en el complejo de bosques de Dadia-Lefkimi-Soufli en el noreste de Grecia. *Circaetus gallicus* anida usualmente en árboles de *Pinus brutia* 83% los cuales fueron dominantes (87%) o intermedio (13%) en el dosel. La mayoría de los nidos se encontraron en los árboles mas grandes en términos de altura ($\bar{x} = 13.8 \pm 0.4$ m, \pm SE) en los rodales. Los nidos fueron localizados en la parte baja y el tercio medio del dosel a una altura media de 8.6 ± 0.41 m en ramas horizontales a una distancia media de 133 ± 12.4 cm del tronco. Se detectó la tendencia de construir los nidos en el costado sur del dosel (mean angle = 178° , angular deviation $s = 58^\circ$). *Circaetus gallicus* seleccionó árboles que le proporcionaron un acceso fácil, como también protección de los depredadores y del inclemente clima.

[Traducción de César Márquez]

The Short-toed Eagle (*Circaetus gallicus*) is a tree-nesting accipitrid (Cramp and Simmons 1980), nesting in a variety of forest types, such as open coniferous forests in France (Thiollay 1968), dense

evergreen oak and mixed deciduous woodland in central Italy (Petretti 1988), mixed conifer-deciduous forests in north-western Italy (Bocca 1989), and dry pine forests with mosses (*Sphagnum* spp.) in the ground layer in Belarus (Ivanovsky 1992). Despite considerable interest in the ecology of Short-toed Eagles in Mediterranean countries, few studies have been conducted to describe the structure of nest trees favored by the species (Petretti

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1988, Vlachos and Papageorgiou 1994). No previous studies have been attempted to describe and compare actual nest trees with available trees.

A detailed analysis of Short-toed Eagle nest trees in the Dadia-Lefkimi-Soufli forest complex was carried out to determine the most important characteristics determining the choice of nest trees. The aims of this study were to describe nest structure and to evaluate nest-tree characteristics of Short-toed Eagles by comparing actual nest trees with randomly-selected trees.

STUDY AREA

The study was conducted in the Dadia-Lefkimi-Soufli (D-L-S) forest complex, in the central part of Evros Prefecture, northeastern Greece (40°59'–41°15'N, 26°19'–26°36'E). The region is on the eastern edge of the Rodopi mountain chain in western Thrace. Elevations range from 20–700 m and steep-sided valleys crisscross the area. The climate is submediterranean and mean monthly temperatures in the area range from 25°C in July to 4°C in January. Mean annual precipitation is 664 mm. Northerly winds predominate during the year following the north-south orientation of the Evros valley.

The structure and composition of the vegetation in the D-L-S forest complex are the result of a combination of climate, soils, and intensive past human influence (Dafis 1973). The study area is covered by a mosaic of different habitat types, such as agricultural lands, grasslands, shrublands, rocky areas, pine forests, oak forests, degraded oak forests, and mixed pine-oak forests. The main overstory tree species are pines, including Calabrian pine (*Pinus brutia*) and black pine (*P. nigra*). The understory is mixed with pines, oaks (*Quercus conferta*, *Q. pubescens*, *Q. sessiliflora*, and *Q. cerris*), and various shrub species (*Phyllirea media*, *Arbutus andrachne*, *Erica arborea*, *Juniperus oxycedrus*, *Carpinus orientalis*, *Ostrya carpinifolia*, and *Fraxinus ornus*). Approximately 19.5% (7250 ha) of the 37 156 ha study area consists of two core areas that were established as protected areas for birds of prey in 1980.

The study area supports a remarkable diversity of wildlife including Black Vultures (*Aegypius monachus*), Griffon Vultures (*Gyps fulvus*), Lesser Spotted Eagles (*Aquila pomarina*), Imperial Eagles (*Aquila heliaca*), Booted Eagles (*Hieraaetus pennatus*), wolves (*Canis lupus*), jackals (*Canis aureus*), wild cats (*Felis sylvestris*), brown hares (*Lepus europaeus*), wild boars (*Sus scrofa*), large whip snakes (*Coluber jugularis*), grass snakes (*Natrix natrix*), dice snakes (*Natrix tessellata*), nose-horned vipers (*Vipera ammodytes*), and green lizards (*Lacerta viridis*) (Bakaloudis et al. 1998).

METHODS

As many occupied Short-toed Eagle territories as possible were located in the study area during the 1996–97 field seasons using (a) historical descriptions of traditional nesting sites, (b) territorial behaviors of breeding pairs noted from high vantage points, and (c) extensive exploratory surveys on foot (Fuller and Mosher 1987). A total of 29 nests were located in 22 Short-toed Eagle ter-

ritories including occupied and old nests. Data on nest-tree characteristics were collected during August and September of 1996–97 after fledging. We recorded the following information to describe each nest tree: tree species, crown class (dominant, intermediate, or suppressed), trunk shape (straight, slightly crooked, crooked, forked, pitchforked, or without top), and canopy shape (condensed, dense, slack, or light). The condition of nest trees was described as good, medium (evidence of fire on bark), or bad (both evidence of fire and epiphytic growth). Nest-tree branches were measured and classified according to their density (I—>20 branches on the trunk, II—10–20 branches on the trunk, or III—<10 branches on the trunk) and their size as (thick—>50% of branches with a diameter >12 cm, medium—>50% of branches with a diameter 8–12 cm, or thin—>50% of branches with a diameter <8 cm). Diameter at breast height (dbh) was measured using a dbh tape and the age was determined using an increment core by counting growth rings. Height of nest trees, height of nests above ground, and height to living canopy were measured with a Blumme-Leiss altimeter (accuracy ± 0.25 m). Canopy height of nest trees was estimated by subtracting the height of the bottom of the canopy to the ground from the height of the tree. Each nest was assigned to the lower, middle, or upper third of the canopy.

In order to compare nest-tree characteristics within the same forest stand, the same number (29) of nonnest trees were randomly selected from neighboring areas. Each random tree was situated from 70–400 m from nest trees. Three steps were followed to establish each random tree. First, the area centered on the nest tree was divided into four quadrants (1 = northeast, 2 = southeast, 3 = southwest, and 4 = northwest) and one of these was randomly selected. Secondly, two randomly-selected numbers between 0–400 were selected to calculate the distance of the random point along the north-south axis and the east-west axis. The intersection of lines extending from these points identified the location of the center of the random tree. Finally, the closest dominant tree to this centered point that was similar in dbh with the nest tree was selected and defined as the random nest tree (Titus and Mosher 1981). When random points identified points in nonforested areas such as grasslands, shrublands, and/or cultivated areas, or in an area with only young trees, they were rejected and the above procedure was reinitiated. The same measurements were made on the randomly-selected trees as nest trees, apart from variables concerning nest characteristics.

Nest features were described quantitatively in terms of the distance to the trunk of the tree in cm, the diameter of branches supporting nests against trunks in cm, maximum and minimum diameter axis of nests in cm, depth of nest cups in cm, and the height of the nest in cm. Nest orientation was determined as the mean flying direction to and from the nest, and nest orientation in relation to trunk was determined as the angle between a line joining the nest with the trunk and magnetic north. Nest orientation and nest orientation in relation to the tree trunk were measured with a compass, recording the angle in degrees from magnetic north.

All variables were tested for heterogeneity of variances using Bartlett's test (Zar 1996) and for normality using

Table 1. Characteristics of 29 Short-toed Eagle nests in the Dadia-Lefkimi-Soufli forest complex, northeastern Greece.

VARIABLE	MEAN \pm SE	RANGE	CV
Height of nest above ground (m)	8.67 \pm 0.41	5.5–12.25	20.47
Diameter of branch supporting the nest (cm)	12.46 \pm 0.91	7.5–26	31.71
Distance from trunk (cm)	133.6 \pm 12.4	45–231	38.72
Diameter of nest (cm) max.	61.75 \pm 1.42	8–74	10.26
Diameter of nest (cm) min.	48.44 \pm 1.06	40–59	9.52
Depth of nest-cup (cm)	7.17 \pm 0.43	5–13	26.63
Height of nest (cm)	17.13 \pm 0.93	12–26	23.74
Orientation of nest in relation to trunk (°)	178		
Orientation of nest (°)	171		

Anderson-Darling test. Variables that did not meet the assumptions of homoscedasticity and normality were log-transformed prior to parametric analysis. Normally-distributed variables were analyzed using paired-sample *t*-tests, but those not meeting normality assumptions after transformation were analyzed using the nonparametric equivalent Wilcoxon matched-pair test. Nominal variables were compared using chi-square analysis. We used Kolmogorov-Smirnov tests to test for uniformity in nest location in nest trees. Variables expressed as percentages were arcsine transformed to standardize variance. Circular variables were analyzed using Rayleigh's *z* test for circular uniformity (Batschelet 1981, Zar 1996). All statistical analyses were performed using the Minitab statistical software (version 12) and differences were considered significant with $\alpha = 0.05$.

RESULTS

Three types of Short-toed Eagle nests were recorded in the study area according to their position within the canopy of nest trees. Type I nests were located in the lower third of the canopy on large, horizontal forked branches and away from trunks. Type II nests were similar, but were located in the middle third of the canopy, and Type III nests were located on the top of relatively-flat canopies near to trunks and open from above. Nests were not distributed uniformly across the three nest types (Kolmogorov-Smirnov test; $D_{\max} = 7$, $P < 0.05$) and were more often located in the lower or middle third than the upper third of the canopy.

Short-toed Eagles had a tendency to build nests on the south-facing sides of the canopy (mean angle = 178° , angular deviation $s = 58^\circ$, measure of concentration $r = 0.49$; Table 1), which was significantly different from a uniform distribution (Rayleigh's test: $z = 6.84$, $P < 0.001$; Fig. 1a). The position of each nest offered incoming eagles a particular direction of approach to the nest. The mean orientation of nests was also south (mean

angle = 171° , $s = 53^\circ$, $r = 0.57$) and the distribution of orientation deviated significantly from random (Rayleigh's test: $z = 9.34$, $P < 0.001$; Fig. 1b). Nests generally were constructed using dead pine twigs, with or without needles, and oak twigs measuring 5–15 cm long and 1–3 cm in diameter. Nest cups were lined with green pine needles and green oak leaves. Materials were added to nests by adult eagles during the breeding season until young eagles fledged from nests. Nests measured on average $61.7 \pm 1.4 \times 48.4 \pm 1.1$ cm ($N = 29$). Short-toed Eagles tend to build new nests each breeding season. In a sample of 35 nesting attempts in the study area during 1996–97, seven pairs repaired and reused the same nest for two consecutive years and three pairs used the same nest for more than two years (unpubl. data).

Short-toed Eagles nested exclusively in Calabrian (83%) and black (17%) pines. All nest trees were alive and fell into the largest diameter size classes. The structure of nest trees was similar to random nest trees (Table 2). We could not detect a difference between nest tree and randomly-selected trees in terms of their dbh, height, canopy height, or age. Nest trees were either dominant (87%) or intermediate (13%) in the canopy; random trees were all dominant (2×2 contingency test, $\chi^2 = 2.071$, $df = 1$, $P = 0.150$). Nest trees had either slightly crooked (90%) or straight (10%) trunks, which was not significantly different from random trees (93% slightly crooked, 7% straight) (2×2 contingency test, $\chi^2 = 0.25$, $df = 1$, $P = 0.61$). Additionally, there were no differences between nest trees and randomly-selected trees in canopy shape (2×3 contingency test, $\chi^2 = 3.39$, $df = 2$, $P = 0.18$) or the condition of the trunk (2×3 contingency test, $\chi^2 = 0.9$, $df = 2$, $P = 0.63$). However,

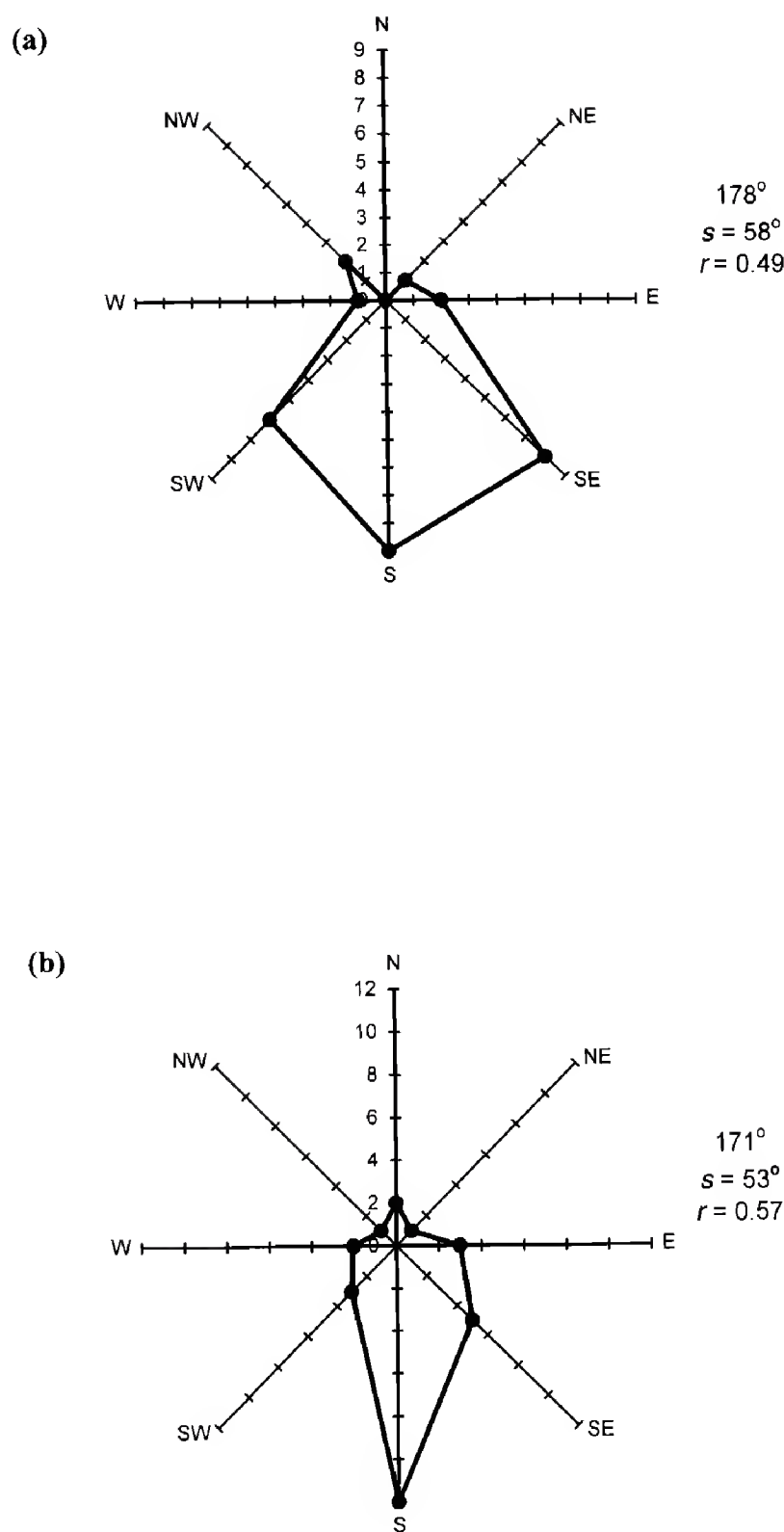


Figure 1. (a) Orientation of Short-toed Eagle nests in relation to nest-tree trunk and (b) orientations of flight path of Short-toed Eagles to and from nests in the Dadia-Lefkimi-Soufli forest complex ($N = 29$).

the majority of nest trees had many (42%) and some (55%) branches, as opposed to random trees which had only some (65%) and few (28%) branches (2×3 contingency test, $\chi^2 = 12.84$, $df = 2$, $P = 0.002$). Branches were also thicker in nest trees than in random trees (2×3 contingency test, $\chi^2 = 9.68$, $df = 2$, $P = 0.008$).

DISCUSSION

Short-toed Eagles were found to use mostly Calabrian (83%) and black (17%) pines for nesting

Table 2. Characteristics of 29 Short-toed Eagle nest trees and 29 randomly-selected mature trees in the Dadia-Lefkimi-Soufli forest complex, northeastern Greece ($\bar{x} \pm SE$). P -value indicates statistical significance of difference between the pairs of means.

VARIABLES	NEST TREE	RANDOM TREE	P-VALUE
dbh (cm)	49.7 ± 1.6	47.9 ± 0.6	0.66 ^a
Height (m)	13.8 ± 0.4	14.2 ± 0.4	0.38
Canopy height (m)	5.8 ± 0.3	6.0 ± 0.2	0.38
Age (years)	87.5 ± 3.1	85.3 ± 3.0	0.51

^a Value based on paired sample Wilcoxon test.

in our study area. Calabrian pine trees generally have only a few, thick branches and an oval-shaped canopy. Black pines have many more and thinner branches with a relatively flat canopy. These differences may explain the Short-toed Eagle's preference for Calabrian pines for nesting. In the same study area, similar findings were also demonstrated by Vlachos and Papageorgiou (1994) who found that 80% and 20% of nests were built on Calabrian and black pines, respectively. In Belarus, Short-toed Eagles nest exclusively in pines (Ivanovsky 1992). In northwestern Italy, they nest in *Larix decidua* and *Pinus sylvestris* (Bocca 1989) and in central Italy they nest in evergreen oak and deciduous trees (Petretti 1988).

All nest trees were dominant with mean height and mean height of canopy of 13.8 and 5.8 m, respectively. Nest trees were also mature ranging from 72–135-yr old and they belonged to the highest diameter size classes with a mean dbh of 49.7 cm. Short-toed Eagles showed a preference for building their nests in trees containing thicker branches and >10 branches per trunk. Trees with this structure probably provide greater shelter from predators and inclement weather while, at the same time, provide support for nests (Solonen 1982). Such trees are the result of a lack of competition during early successional stages (Dafis 1990) or from varying intensities of competition experienced over time (Begon et al. 1996).

Short-toed Eagles preferred to build their nests on the south-facing side of the canopy of nest trees. We suggest several reasons they do this. First, the strong relationship between nest position in relation to trunk and slope orientation offers a particular direction for adults to access nests (Newton 1979, Sieg and Becker 1990) and provides a favorable setting for fledglings when they first fly from

nests. Petretti (1988) also noted that 42.8% of Short-toed Eagle nests in Italy were situated on lateral branches overlooking steep slopes. Secondly, a preferred orientation for nests has also been observed in several raptors and may be related to breeding performance (Vinuela and Sunyer 1992) by providing a favorable environment both for the incubating female and nestlings. The main meteorological factors that might influence nest orientation and reproductive success are temperature early in the breeding season, direct solar radiation during hotter days, and avoidance of other inclement conditions. In D-L-S forest complex, Short-toed Eagles probably gain warmth in the beginning of breeding season when temperatures are still low by situating nests to the south sides of nest trees. Similarly, Ivanovsky (1992) in Belarus, found that nests were directed towards the south or southeast when they were situated below the top of trees. Mosher and White (1976) in Alaska and Poole and Bromley (1988) in the central Canadian Arctic noted the tendency for Golden Eagles (*Aquila chrysaetos*) to place their nests in a southeasterly direction and Buchanan et al. (1993) have recorded a mean southeasterly direction for Spotted Owl (*Strix occidentalis*) nests in the Cascade Mountains in Washington for Spotted Owl nests. Additionally, Tjernberg (1983) in Sweden, has mentioned the preference of Golden Eagles to breed on cliffs facing south or southwest.

Eighty-six percent of the nests were located within the foliage of nest trees on large horizontal branches at a mean distance of 133 cm from trunks. Shadowed by a roof of branches from above, these nests probably provide both concealment from other avian predators (Newton 1979) and direct insulation from the sun. Short-toed Eagles build their nests in foliage to protect incubating females, eggs, and nestlings from aerial avian predators (e.g., Eagle Owls [*Bubo bubo*], Common Ravens [*Corvus corax*], and Hooded Carrion Crows [*Corvus corone cornix*]), which were common in the study area. In addition, branches above nests provide cover from direct solar radiation minimizing thermal stress in newly-hatched nestlings, especially during the hottest days when, in some cases, the temperature rises to 40–43°C.

In our study area, the predominant winds are northerly and the majority of the storms arrive from the north (Flokas 1990). Overall, the placement of nests by birds opposite to prevailing winds and storms may be critical to avoid the most in-

clement weather (Colias and Colias 1984). In the Doñana National Park, Spain, where westerly winds prevail, Black Kites (*Milvus migrans*) build their nests on the leeward sides of tree crowns maximizing the sheltering effect of trees (Vinuela and Sunyer 1992). At Sagehen Creek in California, where inclement weather is mainly from the south, American Kestrels (*Falco sparverius*) situate their nests to avoid this cold direction (Balgooyen 1976, 1990, Raphael 1985). Similarly, Olsen and Olsen (1989) in Canberra, Australia, noted that only 10.3% of Peregrine Falcon (*Falco peregrinus*) nests faced southwest where most inclement weather originated.

In our study, nest features of Short-toed Eagles agreed with those reported in previous studies. Newton (1979), Petretti (1988), and Vlachos and Papageorgiou (1994) noted the tendency for Short-toed Eagles to build small nests for their body size, and to build a new nest in a different place each year. Petretti (1988) reported a total of 39 nesting attempts, but the same nest was used in two consecutive years twice and for three consecutive years only once. Ivanovsky (1992) reported that each pair had 1–9 alternate nests, and the distance between them varied from 300–1500 m. Eagles in our study differed in that they tended to maintain the same nests for longer periods of time, or to use another nest in close proximity to the first. This may have been due to nest site competition with other raptors. The D-L-S forest complex supports a diverse concentration of raptors which possibly creates strong interspecific competition for nesting sites (Vlachos 1989). Another explanation is that Short-toed Eagles are possibly at carrying capacity in the D-L-S forest complex (Hallman 1979) and so remain, year after year, at the same nest sites because no other sites are available.

We observed Short-toed Eagles frequently carrying green twigs to their nests, a behavior that has also been noted by Petretti (1988). Newton (1979) reported this habit for other raptors, and many explanations including nest sanitation and the maintenance of optimum humidity have been suggested for this behavior. The most widely accepted explanation is that raptors bring green vegetation to their nests to advertise territory occupancy (Newton 1979). A further explanation is that the continual addition of nesting material increases the size of the nest to accommodate the increasing size and activity of the nestlings, particularly when they begin to exercise their wings (Newton 1979). Perhaps

this is more important for Short-toed Eagles because they build very small nests in comparison to their size.

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ARE NORTHERN SAW-WHET OWLS NOMADIC?

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ABSTRACT.—The first known nesting of a Northern Saw-whet Owl (*Aegolius acadicus*) in the Snake River Birds of Prey National Conservation Area occurred in a nest box in 1986, 4 yr after nest boxes were constructed in the study area. Occupancy of nest boxes by Northern Saw-whet Owls varied substantially over the next 13 yr (0–8 nests per yr). The number of mice counted on nocturnal surveys fluctuated widely during this same period, and the annual number of Northern Saw-whet Owl nests in the boxes was positively correlated with an index of mouse abundance. Only one of the 52 breeding adults that we banded was recaptured in a subsequent year, and none of the 139 nestlings produced in the boxes was reencountered. A male that we banded at a nest in April 1990 was found dead in British Columbia in January 1993, more than 900 km NNW of our study area. Data from the Bird Banding Laboratory were insufficient to evaluate breeding-site fidelity because few researchers have banded adult Northern Saw-whet Owls at nests. Northern Saw-whet Owls seem to exhibit some of the characteristics associated with nomadism in birds (e.g., high fecundity and low survival), but they differ from typical nomadic species because they do not specialize on cyclic prey. We suggest that Northern Saw-whet Owls are nomadic in some parts of their range, settling to breed in areas of high food abundance that they encounter during the nonbreeding season.

KEY WORDS: *Northern Saw-whet Owl*; *Aegolius acadicus*; *nomadism*; *breeding biology*; *Idaho*.

Es *Aegolius acadicus* una especie nomada?

RESÚMEN.—El primer registro de un *Aegolius acadicus* en anidación en el área de conservación del Snake River ocurrió en una caja de anidación en 1986, 4 años después que las cajas fueron construidas en el área de estudio. La ocupación de las cajas por los buhos varió substancialmente en los próximos 13 años. (0–8 nidos por año). El número de ratones contabilizados de noche fluctuó ampliamente durante este mismo período y el número anual de nidos de buhos en cajas fue positivamente correlacionado con el índice de abundancia de ratones. Solo uno de los 52 adultos en reproducción anillado, fue recapturado y ninguno de los 139 pichones producidos en las cajas de anidación fue reencontrado. Un macho que fue anillado en el nido en abril de 1990 fue encontrado muerto en Columbia Británica en enero de 1993, a mas de 900 km NNW, del área de estudio. Los datos del laboratorio de anillación fueron insuficientes para evaluar la fidelidad al territorio de reproducción debido a que pocos investigadores han anillado adultos de *Aegolius acadicus* en los nidos. *Aegolius acadicus* parece mostrar algunas de las características asociadas con el nomadismo en las aves (e.g., alta fecundidad y baja sobrevivencia), pero difieren de las especies nómadas típicas debido a que no se especializan en una presa cíclica. Sugerimos que los buhos son nómadas en parte de su rango, estableciéndose para reproducirse en áreas de alta abundancia de comida que encuentran durante la estación no reproductiva.

[Traducción de César Márquez]

The raptors nesting in the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho have been under intensive study since the mid-1970s (USDI 1979). Through 1985, six species of owls were known to nest in the area: Barn Owl (*Tyto alba*), Western Screech-Owl (*Otus kennicottii*), Great Horned Owl (*Bubo virginianus*),

Burrowing Owl (*Athene cunicularia*), Long-eared Owl (*Asio otus*), and Short-eared Owl (*A. flammeus*). The first three species are permanent residents in the NCA, the Burrowing Owl is a typical migrant, and the two species of *Asio* are year-round residents in some years and migrants in others (J.S. Marks and J.H. Doremus pers. obs.).

The first known nest of a Northern Saw-whet Owl (*Aegolius acadicus*) in the NCA occurred in a nest box in 1986, 4 yr after boxes were constructed in the study area. In marked contrast to the six species of owls that occur regularly in the NCA, the presence of nesting Northern Saw-whet Owls varied substantially over the next 13 yr (0–8 nests per yr). This variation in numbers, combined with a nearly complete lack of recaptures of adults, led us to speculate that Northern Saw-whet Owls are nomadic in the NCA.

Many species of birds exhibit strong breeding-site fidelity, remaining in or returning to the same breeding places year after year (Andersson 1980). Site fidelity may be adaptive because it allows individuals to learn the best places to feed, nest, and avoid predators, which in turn may enhance the ability of territory holders to attract mates (Hinde 1956, Greenwood and Harvey 1976, Greenwood 1980). Nomadism (i.e., lack of breeding-site fidelity) in birds is much less common than site fidelity and tends to be restricted to species that feed on cyclic prey or for which environmental variation (e.g., periodic rains) results in large fluctuations in the availability of suitable breeding habitat (Andersson 1980, 1981).

The classic examples of nomadism in birds come from boreal seedeaters such as finches and crossbills that move large distances in response to changing availability of beechmast and conifer seeds (Newton 1972). In owls, nomadism is best known in vole specialists such as Boreal Owls (*Aegolius funereus*), Long-eared Owls, and Short-eared Owls (Wallin and Andersson 1981, Village 1987, Korpimäki and Norrdahl 1991), although documentation of the same individuals breeding in vastly different locations is rare. Several female Boreal Owls have been captured at nests more than 500 km apart in different years (Wallin and Andersson 1981, Korpimäki et al. 1987), but the extent of nomadism in this species varies widely among populations, and individuals may remain on the same home ranges for two or more years in succession (Korpimäki et al. 1987, Hayward et al. 1993). In short, compared with “classic” nomadism exhibited by boreal seedeaters, the owl species noted above seem to be “periodically” nomadic.

The Northern Saw-whet Owl is common in forested habitats across the northern United States and southern Canada. Despite its abundance, relatively little is known about its breeding biology (Cannings 1993). In this paper, we present data to

suggest that Northern Saw-whet Owls are nomadic in southwestern Idaho. If we are correct, then our study birds would constitute the only known example of nomadism in a strigid that does not specialize on cyclic prey.

STUDY AREA AND METHODS

We studied breeding Northern Saw-whet Owls in the NCA in southwestern Idaho from 1986–99. The NCA is a shrubsteppe desert dominated by big sagebrush (*Artemisia tridentata*). Compared with typical breeding habitat for Northern Saw-whet Owls (i.e., coniferous forest), trees are scarce and are confined to riparian areas and human settlements. All of the owls that we studied bred in nest boxes placed in willows (*Salix* spp.), Russian olives (*Elaeagnus angustifolia*), and black locusts (*Robinia pseudoacacia*). We set out boxes in pairs (1–40 m apart) beginning in 1981. Since 1986, when Northern Saw-whet Owls first nested in one of our boxes, two or more boxes have been available at 25–47 sites each year along 95 linear km of the Snake River and its tributaries.

To assess the availability of small mammals, we conducted nocturnal surveys in the NCA each spring from 1984–94 (see Marks et al. 1989). With the aid of a spotlight, observers in a slowly moving vehicle counted all “mice” seen along 547–709 km of secondary roads. Based on these surveys, we calculated an index of mouse numbers by dividing the total number of mice seen by the total length of roads surveyed each year. No surveys were conducted after 1994.

We captured breeding female owls in nest boxes during the brood-rearing period and caught males at night in mist nets set in front of the boxes. We determined the sex of adults by the presence (females) or absence (males) of an incubation patch. Adults were weighed, measured, and banded at first capture, and nestlings were banded about a week before they left the nest.

We used partial correlation analysis to assess the relationship between the mouse index (log transformed) and the number of owl nests in the boxes and to see whether the number of Northern Saw-whet Owl nests was correlated with the number of Western Screech-Owl nests. All tests were one-tailed because we predicted that numbers of nesting owls of both species would be positively correlated with the mouse index. Similarly, we predicted that the number of nesting Northern Saw-whet Owls would be negatively correlated with the number of nesting Western Screech-Owls in the boxes because Western Screech-Owls are permanent residents in the NCA, and their body mass is two to three times that of Northern Saw-whet Owls (J.S. Marks and J.H. Doremus unpubl. data).

RESULTS

The number of Northern Saw-whet Owl nests in our boxes varied considerably among years, ranging from zero to eight ($\bar{x} = 2.7 \pm 3.09$ [\pm SD]) (Table 1). In contrast, Western Screech-Owls nested in the boxes every year (range 4–13), and the number of nests per year was larger ($\bar{x} = 8.8 \pm$

Table 1. Number of Northern Saw-whet Owl and Western Screech-Owl nests in boxes in the Snake River Birds of Prey National Conservation Area, 1984–99. Pairs of nest boxes were available at 25–47 sites each year. The number of adult Northern Saw-whet Owls captured at nests each year is in parentheses.

YEAR	NORTHERN SAW-WHET OWL	WESTERN SCREECH- OWL
1984	0	7
1985	0	5
1986	1	5
1987	7 (11)	8
1988	0	4
1989	0	6
1990	8 (11)	9
1991	6 (10)	11
1992	7 (5)	13
1993	1	13
1994	0	8
1995	5 (6)	13
1996	3 (4)	11
1997	0	8
1998	0	9
1999	5 (5)	10

2.93) and less variable than that of Northern Saw-whet Owls (Table 1). Rather than the negative relationship that we expected, the number of Northern Saw-whet Owl nests in the boxes was positively correlated with the number of Western Screech-Owl nests in the boxes each year (partial $r = 0.58$, $N = 16$, $P = 0.038$; Fig. 1). Indeed, in several cases Northern Saw-whet Owls nested in boxes within occupied Western Screech-Owl territories. Thus, the presence of Western Screech-Owls appeared to have no negative effect on yearly fluctuations in the number of Northern Saw-whet Owl nests in the boxes.

The number of mice counted during nocturnal surveys also varied substantially from year to year (Table 2). The years with the highest mouse numbers tended to coincide with the highest numbers of nesting Northern Saw-whet Owls in the boxes (Tables 1, 2), and the number of Northern Saw-whet Owl nests was positively correlated with the mouse index during the years that we had data on small mammals (partial $r = 0.69$, $N = 11$, $P = 0.013$; Fig. 2a). In contrast, no significant correlation existed between the mouse index and the

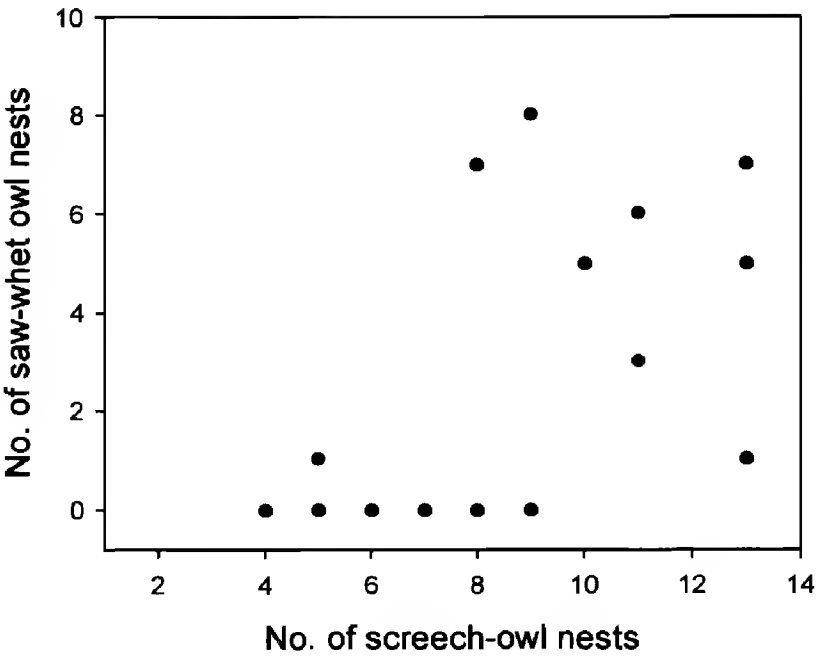


Figure 1. Relationship between the number of Northern Saw-whet Owl nests in boxes and the number of Western Screech-Owl nests in boxes, Snake River Birds of Prey National Conservation Area, 1984–99. Only 15 points are shown because two were identical.

number of Western Screech-Owl nests in the boxes (partial $r = -0.28$, $N = 11$, $P = 0.21$; Fig. 2b).

We caught 52 adult Northern Saw-whet Owls (29 females, 23 males) at the 43 nests that we monitored (Table 1). Only one returned to breed in a subsequent year, a female that nested in boxes 360 m apart in 1990 and 1991. A male that bred successfully in the study area in 1990 was found freshly

Table 2. Results of nocturnal spotlight surveys for small mammals in the Snake River Birds of Prey National Conservation Area, 1984–94 (no surveys were conducted after 1994).

YEAR	MICE ^a	SURVEY LENGTH (km)	MICE/km
1984	2	547	0.004
1985	30	547	0.055
1986	4	547	0.007
1987	293	612	0.479
1988	20	612	0.033
1989	43	709	0.061
1990	146	700	0.208
1991	24	604	0.040
1992	47	603	0.078
1993	15	660	0.023
1994	21	659	0.032

^a Total number counted on surveys each year. “Mice” includes *Perognathus parvus*, *Onychomys leucogaster*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Microtus montanus*.

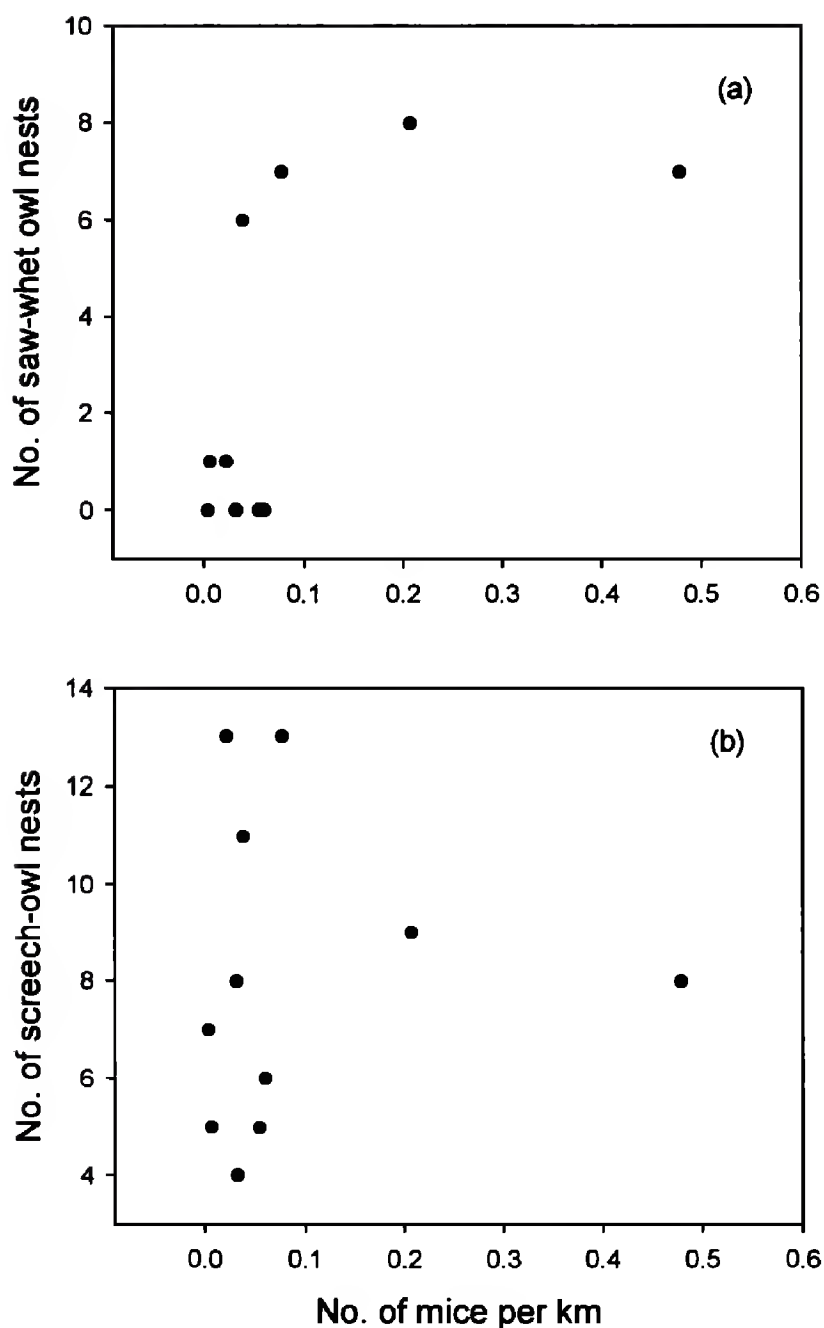


Figure 2. Relationship between the mouse index and the number of Northern Saw-whet Owl nests in boxes (a) and the number of Western Screech-Owl nests in boxes (b), Snake River Birds of Prey National Conservation Area, 1984–94.

dead in British Columbia in January 1993, approximately 920 km NNW of the NCA. No other adults that we banded in the study area have been reencountered, nor have we reencountered any of the 139 nestlings produced in the boxes. Nesting success was rather high, with 29 of 42 nests (69%; one nest was not monitored completely) producing one or more young that survived to leave the nest (\bar{x} = 3.3 young per nesting attempt and 4.8 per successful nest).

In contrast to the situation with Northern Saw-whet Owls, we made hundreds of recaptures of adult Western Screech-Owls, which occupied their breeding territories year-round (indeed, once a Western Screech-Owl settles on a breeding site, it

typically remains there for life). Western Screech-Owl nests were not confined to boxes; some occurred in natural cavities in trees and cliffs, and one pair nested in an old Black-billed Magpie (*Pica hudsonia*) nest (J.S. Marks and J.H. Doremus pers. obs., Marks 1983). We have never found a Northern Saw-whet Owl nest anywhere in the NCA except in a nest box, nor have we heard males singing from tree groves that did not contain a box. Thus, we suspect that few Northern Saw-whet Owls nest in sites other than our boxes.

DISCUSSION

The Northern Saw-whet Owls that we studied appeared to be nomadic. Turnover among breeding adults was high, and no juveniles were known to have returned to the study area to breed. The best evidence for nomadism would be the capture of marked individuals at widely separated breeding sites in different years. Such evidence is absent from banding records, although we note that the banding data are not ideal for assessing breeding-site fidelity.

Our review of the 1276 reencounters (through August 1999) of Northern Saw-whet Owls in the database of the USGS Bird Banding Laboratory showed that less than 3% were of birds banded during the breeding season, and we found no records of birds banded at a nest in one year and recaptured at a distant site in a subsequent breeding season. Indeed, aside from the instance we documented in the NCA, the only known cases of breeding-site fidelity in Northern Saw-whet Owls have come from British Columbia, where 5 of 36 breeding adults (two females, three males) banded over an 8-yr period returned to the same or adjacent territories in subsequent years (Cannings 1993).

Predatory birds that exhibit nomadism typically feed on cyclic prey, and in theory they should produce large clutch sizes, reproduce at one year of age, and have high juvenile survival and low adult survival (Andersson 1980). Northern Saw-whet Owls in the NCA have high fecundity (typical clutches contain 6–7 eggs, which is at the high end of the range of clutch sizes for the continent; Cannings 1993), but they do not specialize on cyclic prey. Rather, their diet consists of a mixture of house mice (*Mus musculus*), harvest mice (*Reithrodontomys megalotis*), montane voles (*Microtus montanus*), and deer mice (*Peromyscus maniculatus*) (Marks and Doremus 1988, Rains 1997). The abun-

dance of these prey species in the NCA varies unpredictably rather than in a cyclic pattern. Elsewhere in the range of Northern Saw-whet Owls, vole populations can be cyclic. However, voles seldom comprise a major portion of the diet during the breeding season (Marks and Doremus 1988, Swengel and Swengel 1992, Cannings 1993). Northern Saw-whet Owls probably reproduce at one year of age, but the age of first breeding is not known for wild birds (Cannings 1993). In addition, little is known about annual survivorship of adults or juveniles, although adult survival appears to be low (ca. 50%; Cannings 1993). Thus, Northern Saw-whet Owls exhibit some of the characteristics of nomadic species, but they differ fundamentally from typical nomads in that they do not specialize on cyclic prey.

Nomadism in owls has been documented most thoroughly in the Boreal Owl (e.g., Wallin and Andersson 1981, Löfgren et al. 1986, Korpimäki et al. 1987). Male Boreal Owls in Fennoscandia tend to remain on their territories year-round, whereas females are more likely to disperse between breeding sites, especially during lows in the vole cycle (Löfgren et al. 1986, Korpimäki et al. 1987). Nomadism and site fidelity have been documented in both sexes of Boreal Owls in Idaho, but the tendency toward nomadism is strongest in females (Hayward et al. 1993:33–35). Thus, unlike the situation in the NCA, where both sexes of Northern Saw-whet Owls almost never display site fidelity, nomadism in Boreal Owls is confined mostly to females and occurs in some years but not others.

Aside from our study population, the only previous hints that Northern Saw-whet Owls are nomadic have come from studies of vocal activity in Colorado (Palmer 1987) and Wisconsin (Swengel and Swengel 1995). In the Colorado study, annual changes in the number of singing birds corresponded with changes in the numbers of voles in the area. In Wisconsin, nightly surveys conducted in late winter and early spring over a 10-yr period revealed a fairly strong 4-yr "cycle" in the amount of singing by adults. Swengel and Swengel (1995) noted that the vole cycle was a possible explanation for the pattern in vocal activity that they observed. Neither study involved finding nests and trapping adults, however, so it is difficult to determine the extent to which changes in vocal activity translate to actual changes in the presence of breeding birds.

Lacking the proof that would be provided if our

birds had been captured outside of the NCA in subsequent breeding seasons, two alternative hypotheses could explain the apparent lack of site fidelity that we observed. First, the NCA may be a "sink" in which Northern Saw-whet Owls have low annual survival relative to those nesting elsewhere. We have no way to test this hypothesis, but the presence of one of our males in Canada three years after breeding in the NCA, and the apparently high reproductive success of Northern Saw-whet Owls in our study area (see Cannings 1993), argue against the notion that these birds constitute a sink population. Second, we may have failed to detect adults that returned to breed in the NCA because they used natural cavities. We have not conducted systematic surveys of tree cavities throughout the NCA, but as noted above, we have never heard Northern Saw-whet Owls singing in areas that did not contain nest boxes. We suspect that few owls nest in natural sites relative to the number that use our boxes. Nonetheless, it is possible that we have missed some nests in natural sites and that site tenacity by Northern Saw-whet Owls is more prevalent in the NCA than we believe.

If we are correct in our assertion that Northern Saw-whet Owls are nomadic in southwestern Idaho, then these birds would constitute the first known case of nomadism in a species of owl that does not specialize on cyclic prey. Given the apparent geographic variation in nomadism exhibited by Boreal Owls (Korpimäki et al. 1987), it is likely that the incidence of nomadism in Northern Saw-whet Owls varies geographically. The shrubsteppe desert of southwestern Idaho is not typical breeding habitat for Northern Saw-whet Owls. Indeed, without the presence of nest boxes, we suspect that few Northern Saw-whet Owls would breed in our study area. Northern Saw-whet Owls have probably wintered in the NCA for many years, but the availability of nest boxes has only recently made the area suitable for nesting. We suggest that Northern Saw-whet Owls are nomadic in some parts of their range, settling to breed in the same areas in which they winter or migrate during years when food availability is high. Long-term banding efforts at nests, coupled with monitoring of prey availability, will be necessary to thoroughly address the question of nomadism in Northern Saw-whet Owls.

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RELATIONSHIP BETWEEN RAPTORS AND RABBITS IN THE DIET OF EAGLE OWLS IN SOUTHWESTERN EUROPE: COMPETITION REMOVAL OR FOOD STRESS?

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ABSTRACT.—I tested whether higher predation rates by Mediterranean Eagle Owls (*Bubo bubo*) on other species of raptors was associated with lower availability of the most profitable prey for this owl, the European rabbit (*Oryctolagus cuniculus*). Additionally, I investigated whether the main force regulating the importance of raptors in the diet of Eagle Owls was the acquisition of food or the removal of competition. Rabbits are the staple prey of this species in Mediterranean ecosystems of southwestern Europe. My analysis was based on 17 557 prey items from 19 studies of Eagle Owl diet in Spain and France. Rabbits and raptors showed significant inverse relationships, but this trend was not significant when only raptors competing for rabbits were included in the analysis. Thus, trophic diversification when rabbit numbers were low, including changes in the use of the foraging habitat, seemed to be the main explanation for this interaction. Rabbit populations have declined sharply after two outbreaks of viral diseases that have been linked to an increase of other raptors in the diet of Eagle Owls. For this reason, the management of rabbits could benefit the conservation of raptor communities, of which eagle owls are a part.

KEY WORDS: *Eagle Owl*, *Bubo bubo*; *food stress*; *intraguild predation*; *European rabbit*; *Oryctolagus cuniculus*; *Mediterranean*.

Relación entre aves rapaces y conejos en la dieta de *Bubo bubo* en el suroeste de Europa: competencia por remoción o estrés por alimento?

RESÚMEN.—Se exploraron las relaciones entre el conejo (*Oryctolagus cuniculus*) y el resto de las rapaces en la dieta del búho real (*Bubo bubo*) en ecosistemas mediterráneos del suroeste de Europa. Asimismo, se intentó determinar si dicha relación responde simplemente a una búsqueda de presas alternativas o a la eliminación de competidores. Se recopiló bibliografía que incluía 17 557 presas pertenecientes a 19 poblaciones de España y Francia. Fueron halladas correlaciones significativas que relacionaban de forma inversa la contribución de rapaces y conejos a la dieta del ave. Sin embargo, al incluir en los análisis únicamente aves rapaces que pueden competir por el conejo las tendencias no fueron significativas. Se concluyó que existe una respuesta funcional de los búhos reales en áreas con bajos niveles poblacionales de conejo y que la diversificación de la dieta y los cambios en el uso del hábitat de caza, y no la eliminación de competidores, parecen las explicaciones más plausibles para este tipo de interacción. Las densidades de conejo han sufrido un acentuado declive como consecuencia de la mixomatosis y de la neumonía hemorrágica vírica que parece estar determinando una mayor importancia de las rapaces en la dieta de los búhos. Consecuentemente, un adecuado manejo de las poblaciones de conejo podría redundar indirectamente en la conservación de las aves de presa que comparten hábitat con el búho real.

[Traducción del autor]

The role of top predators on food-web structure and predator-prey interactions may have strong implications in conservation and management of both game-species and predator assemblages (Palomares et al. 1995, Litvaitis and Villafuerte 1996). In this sense, raptors killing other raptors has been suggested to affect the structure and other aspects

of population dynamics in bird of prey communities (Mikkola 1976, Rudolph 1978, Hakkarainen and Korpimäki 1996). This ecological process is particularly important when it involves individuals of endangered species as prey, a case in which the death of a few individuals may drive local populations to extinction. There is uncertainty about

whether raptors kill other raptors simply to acquire food or to obtain benefits by removing competitors (Mikkola 1983, Rohner and Doyle 1992). Although experiments are needed, these are difficult with such wide-ranging species. Therefore, analysis of existing empirical data should be encouraged.

Eagle Owls (*Bubo bubo*) are large nocturnal raptors preying on a wide spectrum of species, both in terms of body size and ecological requirements. European rabbits (*Oryctolagus cuniculus*) constitute the preferred prey of this species in Mediterranean habitats of southwestern Europe due to their abundance and the absence of other prey of similar size (Hiraldo et al. 1976, Jaksić and Marti 1984, Donazar et al. 1989). However, rabbit densities vary between areas, specially after outbreaks of viral diseases that have reduced populations (Villafuerte et al. 1995). Eagle Owls feed preferentially on this species in Mediterranean areas whenever it is abundant, but switch to less profitable alternative prey where rabbits are scarce. Thus, rabbit occurrence in the owl's diet may indicate their local availability (Donazar 1989, Serrano 1998).

Numerous studies of Eagle Owls have shown the regular occurrence of raptors in their diet (see review in Mikkola 1983, Penteriani 1996), including young and adults of threatened species (Real and Mañosa 1990, Tella and Mañosa 1993). Eagle owls may act as both predators and competitors with other raptors at a similar trophic level, so intra-guild predation (*sensu* Polis and Holt 1992) could be an explanation for such an interaction. Alternatively, it has been suggested that Eagle Owls in Mediterranean ecosystems feed on a larger proportion of raptors in conditions of food stress resulting from rabbit scarcity (Tella and Mañosa 1993). This hypothesis requires more study of different populations of raptors and their prey to provide additional evidence. If raptors actually compete with Eagle Owls (i.e., those feeding on rabbits are killed when rabbits are scarce), an inverse relationship should occur between their dietary proportions. Alternatively, if food stress as a consequence of rabbit scarcity is the main explanation for Eagle Owls killing other raptors, there should be no relationship between the proportion of raptors competing for food and rabbits in their diet. Thus, studying the dietary contribution of raptors in different scenarios of rabbit availability could improve our understanding of interspecific depredation among raptors. The aim of this paper was to quantify the importance of raptors in the diet

of Mediterranean Eagle Owls and to explore whether higher predation rates on other raptor species are associated with lower availability of rabbits. Additionally, two hypothesis were tested: whether food stress or competition removal is the main force regulating this phenomenon.

METHODS

This paper is based on 19 studies of Eagle Owl diet in Spain and France, which included >200 prey items per study (Table 1). Most of these studies used the analysis of pellets from nestlings and adults to determine the diet which seems to accurately reflect overall owl diet. Numerical and biomass contribution were reported since frequency is important when looking at the number of competitors removed and biomass reflects the energetic yield of each taxonomic group. Percent biomass of each taxonomic group in the diet were calculated following Hiraldo et al. (1975a), Real et al. (1985), and Perrins (1987). A value of 500 g was assigned to each rabbit, as Eagle Owls actively select young and subadult rabbits (Donazar and Ceballos 1989).

Falconiformes are active diurnally, whereas Strigiformes are mainly nocturnal, and frequently share foraging habitats with Eagle Owls. Moreover, nocturnal raptors can be potentially detected by Eagle Owls through their vocalizations. Thus, for statistical analysis, Falconiformes and Strigiformes were considered as two separate groups

RESULTS

Falconiformes and Strigiformes comprised 97 (0.55%) and 223 (1.27%) out of the 17 557 prey items identified. Biomass frequencies were 0.7 and 1.0%, respectively. This included the depredation of 10 species of Falconiformes and six of Strigiformes (Table 2), although at least four other species of Falconiformes (Egyptian Vulture [*Neophron percnopterus*], Bonelli's Eagle [*Hieraetus fasciatus*], Booted Eagle [*Hieraetus pennatus*], and Red Kite [*Milvus milvus*]) have also been reported to be prey of Eagle Owls in Mediterranean ecosystems of Europe (Pérez-Chiscano 1974, Real and Mañosa 1990, Tella and Mañosa 1993). European Kestrels (*Falco tinnunculus*) were the most frequently taken Falconiform, while Little (*Athene noctua*) and Barn (*Tyto alba*) Owls were the most commonly taken Strigiforms (Table 2).

Frequency of occurrence of diurnal raptors and rabbits was negatively related ($r_s = -0.61$, $N = 19$, $P = 0.006$), but this trend was not significant for nocturnal raptors ($r_s = -0.39$, $N = 19$, $P = 0.103$). The contribution of raptor and rabbit biomass to the owl diet was negatively related when analyzed separately (Falconiformes: $r_s = -0.65$, $P = 0.002$; Strigiformes: $r_s = -0.55$, $N = 19$, $P = 0.014$). These results could have been due to the high biomass

Table 1. Numerical (N) and Biomass (B) frequencies of Falconiformes (Falc), Strigiformes (Stri), and European rabbits (Rabb) in 19 populations of Mediterranean Eagle Owls. Sample sizes in each population is given (N).

LOCALITY	FALC		STRI		RABB		N	REFERENCE
	N	B	N	B	N	B		
Bardenas	0	0	3.7	2.0	64.1	85.1	245	1 ^a
Navarra E	0.4	0.7	3.3	2.6	22.7	46.1	958	1 ^a
Navarra W	0.3	1.6	1.6	2.5	10.2	26.9	1355	1 ^a
Ebro N	0.4	1.6	0.9	2.9	5.2	31.3	2141	2 ^a
Ebro S	0.8	1.2	1.9	1.3	33.5	65.5	1529	2 ^a
Murcia	1.4	0.8	1.5	0.6	53.6	66.0	1398	3 ^b
Toledo 1	0.1	0.3	0	0	79	77.5	829	4 ^b
Villuercas	0.3	0.9	0	0	42.4	57.4	361	4 ^b
Málaga	0	0	0	0	61.3	77.6	256	5 ^b
S. Morena	0.2	0.2	0.2	0.1	67.9	76.1	1590	5 ^b
Extremadura	0.2	0.6	0.5	0.4	41.2	53.2	417	5 ^b
Toledo 2	0	0	0.7	0.3	77.1	83.6	266	5 ^b
Salamanca	0.7	1.2	0.1	0.1	25.8	43.3	732	5 ^b
Massif Central	3.2	4.2	6	4.7	15.3	19.0	216	6 ^b
Tarn	1	0.6	1.5	1.0	22.8	25.4	595	7 ^b
Hérault	0.5	1.0	1.4	1.2	26.5	39.2	623	7 ^b
Provence 1	0.6	0.4	1.4	1.4	19	31.2	2923	8 ^b
Vallès	0.3	0.4	0.1	0.3	22.1	34.5	724	9 ^b
Provence 2	0.2	0.2	1.5	0.9	35.8	45.9	399	10 ^b

1 Donázar 1989; 2: Serrano 1998; 3: Martínez et al. 1992; 4: Pérez-Mellado 1980; 5: Hiraldo et al. 1975b; 6: Choussy 1971; 7: Cugnasse 1983; 8: Orsini, 1985; 9: Real et al. 1985; 10: Blondel and Badan 1976.

^a Pellet remains from adults.
^b Pellet remains from adults and nestlings.

Table 2. Number of raptors (N) and numerical (%N) and biomass (%B) frequencies of each species of raptor taken by Eagle Owls in 19 Mediterranean populations. Species competing with Eagle Owls for rabbits are shown (*).

SPECIES	N	%N	%B
<i>Falco tinnunculus</i>	64	20.0	13.2
<i>Falco peregrinus</i>	1	0.3	1.0
<i>Accipiter nisus</i>	4	1.3	0.7
<i>Accipiter gentilis</i> (*)	2	0.6	2.4
<i>Circus aeruginosus</i> (*)	1	0.3	0.6
<i>Circus pygargus</i>	4	1.3	1.2
<i>Buteo buteo</i> (*)	10	3.1	9.8
<i>Milvus migrans</i> (*)	5	1.6	5.1
<i>Pernis apivorus</i>	1	0.3	0.9
<i>Circaetus gallicus</i>	1	0.3	2.1
Unidentified Falconiforms	4	1.3	4.1
<i>Tyto alba</i>	76	23.7	23.4
<i>Strix aluco</i>	28	8.7	12.9
<i>Athene noctua</i>	88	27.5	15.4
<i>Asio otus</i>	23	7.2	6.5
<i>Otus scops</i>	8	2.5	0.7
Total	320	100	100

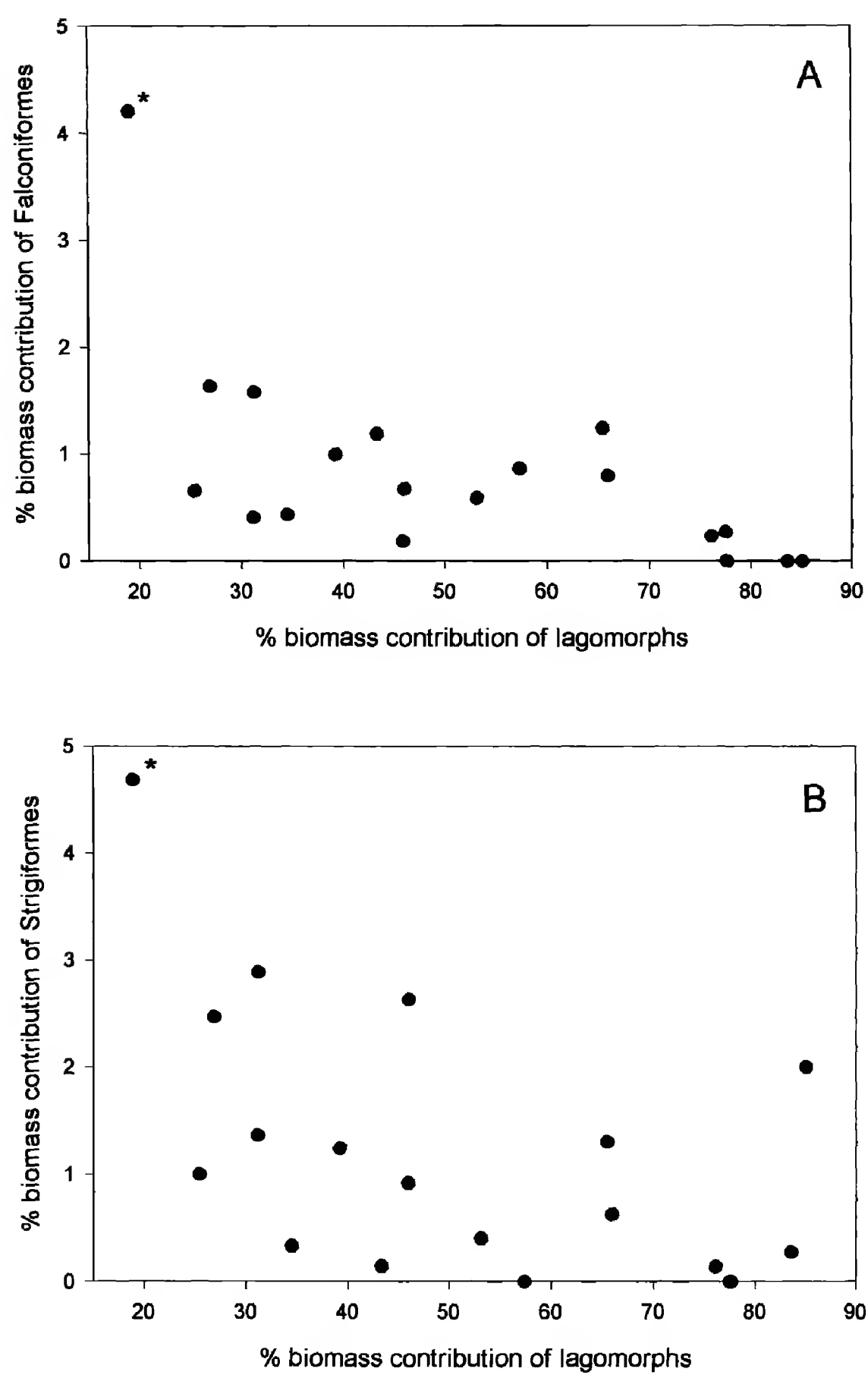


Figure 1. Percent biomass of lagomorphs in relation to percent biomass of Falconiformes (A) and Strigiformes (B) in the diet of 19 populations of Eagle Owls (*Bubo bubo*) in western Palearctic. The symbol * shows the population of Massif Central.

of raptors in the study from the Massif Central (Fig. 1). Removing this sample from the analysis reduced the strength of the relationships, but they were still significant (Falconiformes: $r_s = -0.59$, $P = 0.009$; Strigiformes: $r_s = -0.47$, $N = 19$, $P =$

0.049). Only four species of Falconiformes in these studies may compete with Eagle Owls for rabbits (Table 2; see del Hoyo et al. 1994). After removing the rest from the analysis, the relationship was not maintained when raptor and rabbit contribution

was analyzed (numerical frequencies: $r_s = -0.17$, $N = 19$, $P = 0.484$; biomass frequencies: $r_s = -0.32$, $N = 19$, $P = 0.181$).

DISCUSSION

My results suggest a close relationship between rabbits, the main prey, and raptors in the diet of Eagle Owls. This agreed with Tella and Mañosa (1993) who found that Eagle Owls seemed to take a larger proportion of raptors when rabbits were scarce. The weak relationship between rabbits and raptors competing for food with Eagle Owls suggested a food-searching rather than a competitor-removal process. Moreover, the fact that the species most frequently taken seldom compete for trophic resources with Eagle Owls supported this hypothesis.

Rabbits are social mammals inhabiting flat or gently undulated Mediterranean scrub habitats of the western Palearctic. In areas of high density of rabbits, Eagle Owls seem to concentrate their hunting effort in distinct perches around burrows. In contrast, other types of habitat are exploited in areas with low rabbit densities (Serrano 1998). Eagle Owls discriminate prey by size rather than by a taxonomic criterion, and are capable of killing most Mediterranean raptors. Thus, when rabbits are scarce, Eagle Owls probably search for alternative prey more frequently in habitats used by other raptors for nesting or roosting (e.g., cliffs, woodlands, and river groves). Thus, an increase of raptors in the diet is related to diet diversification as a consequence of low rabbit abundance (see Hiraldo et al. 1976, Donazar et al. 1989, Serrano 1998 for changes in trophic diversity according to rabbit availability).

Rabbits constitute one of the staple food sources for the top predator assemblage of Mediterranean ecosystems in western Europe (Delibes and Hiraldo 1981). Thus, the decline of European rabbits in recent decades as a consequence of human-induced epizootic diseases (first myxomatosis, see Delibes and Hiraldo 1981, and then viral haemorrhagic disease, Villafuerte et al. 1995) has been suggested to affect some threatened species of raptors (e.g., Fernández 1993, Garza and Arroyo 1996, González 1996, Villafuerte et al. 1998, but see Ontiveros and Pleguezuelos 2000). Regardless of the low incidence of raptors in the overall diet of Eagle Owls, my results indicated that low rabbit populations could be influencing the structure of Mediterranean raptor communities and the conserva-

tion of endangered sympatric raptors. In this sense, preliminary results of an ongoing research carried out in eight study areas in the Italian pre-Alps have highlighted a significant effect of Eagle Owl abundance on the pattern of nest dispersion, territory occupation, and productivity of some species in the diurnal raptor assemblage (Sergio et al. 1999a, 1999b). However, to determine the abundance and distribution of other raptors in relation to Eagle Owl diet and rabbit abundance, additional research is needed to assess the impact of this top predator on raptor communities.

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AN EVALUATION OF METHYL ANTHRANILATE, AMINOACETOPHENONE, AND UNFAMILIAR COLORATION AS FEEDING REPELLENTS TO AMERICAN KESTRELS

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ABSTRACT.—A comparison of methyl anthranilate and 4-aminoacetophenone as feeding repellents to a captive colony of American Kestrels (*Falco sparverius*) was made to determine whether aversive conditioning to these chemicals is possible in a bird of prey species. Our results suggested that, while these chemicals seemed to cause some food rejection by kestrels, they did not deter them from eating treated dead, day-old cockerels. A second study using a combination of chemical additives linked to food dyed an unfamiliar color revealed that color, and not the chemicals, was a more aversive agent. This suggested that manipulation of a kestrel's visual perception of a prey item alone had potentially more success than conditioning it to avoid a chemical additive. These results may prove useful in practical applications such as protecting game bird young at wild release sites or domestic homing pigeons associated with a particular home loft. These measures may in turn help to protect birds of prey from persecution as competitors for prey of human economic importance.

KEY WORDS: *American Kestrel; Falco sparverius; conditioned taste aversion; CTA; food choice, appetite suppressant; visual perception; aposmatic coloration.*

Metil antranilato, aminoacetofen y la coloracion inusual como repelentes alimenticios de *Falco sparverius*

RESÚMEN.—Una comparación de metil antranilato y 4 aminoacetofen como repelentes alimenticios de una colonia en cautiverio de *Falco sparverius* fue utilizada para determinar si un acondicionamiento de aversión a estos químicos es posible en una especie de ave rapaz. Nuestros resultados sugieren que mientras estos químicos pudieron haber causado algun tipo de rechazo por los cernícalos, esto no los detuvo de alimentarse de pollos muertos de un día de nacidos. Un segundo estudio utilizando una combinación de aditivos químicos ligados a una comida teñida de un color inusual, reveló que el color y no los químicos obraron mas como agente de aversión. Esto sugirió que la manipulación de la percepción visual de una presa tuvo potencialmente mas éxito que el acondicionamiento para evitar los aditivos químicos. Estos resultados pueden ser útiles en la aplicación práctica como en la protección de juveniles de aves de caza en los sitios de liberación o de palomas mensajeras asociadas a ciertos sitios. Estas medidas pueden a la vez ayudar a proteger a las aves rapaces de la persecución como competidoras de presas de importancia económica.

[Traducción de César Márquez]

Although charismatic and often of high conservation priority, birds of prey are regarded as pests when taking prey of human economic interest, such as when Peregrine Falcons (*Falco peregrinus*) take domestic pigeons (*Columba livia*) (Ratcliffe 1993), Hen Harriers (*Circus cyaneus*) and other raptors kill Red Grouse (*Lagopus lagopus*) (Redpath and Thirgood 1997), and Northern Goshawks (*Accipiter gentilis*) kill Ring-necked Pheasants (*Phasianus colchicus*) (Kenward 1977). Such conflicts of

interest have resulted in the illegal killing of birds of prey (Cadbury 1992, Etheridge et al. 1997). Musgrove (1997) has suggested the use of aversive conditioning to chemical deterrents as an acceptable (in the sense of Liss 1997) way of reducing Peregrine Falcon predation on pigeons and his pilot studies have shown that methyl anthranilate mixed with food causes vomiting in several falcon species, and so was presumably potentially aversive.

Limitations of methyl anthranilate application in

field situations are associated with its volatility and degradation in sunlight (Askham 1992). Isomers of aminoacetophenone appear to be up to 10 times more repellent to European Starlings (*Sturnus vulgaris*) than does methyl anthranilate (Mason et al. 1991), while the importance of intramolecular hydrogen bonds in the different isomers suggests greater repellency (Clark and Shah 1991) and lower vapor pressure (i.e., lower volatility). Thus 4-aminoacetophenone probably combines lower volatility and higher repellency when compared with methyl anthranilate (M. Baldwin pers. comm.).

The use of chemical repellents to instigate chemical aversion conditioning has been used with varying success in the control of many vertebrate pests (Mason 1997) including numerous avian species (Belant et al. 1997, Mason and Clark 1997, Clark 1998). Other workers (Reynolds and Nicolaus 1994, Reynolds 1999) have concentrated on the predation deterrent value of conditioned taste aversion (CTA) and report varying degrees of success in field application.

To date, however, largescale replicated trials of aversive conditioning on a bird of prey species remain untried. Accordingly, this paper reports on assessment of methyl anthranilate and 4-aminoacetophenone as feeding repellents to American Kestrels, a useful raptor model (Bird 1982) and also whether aversive conditioning to these chemicals is possible in this species.

METHODS

Thirty-three adult male, captive-bred American Kestrels at the Avian Science & Conservation Centre (ASCC) of McGill University were housed individually in open-fronted, wooden cages (60 × 40 × 48 cm) during April 1998 in an ambient temperature room on a 14 hr/10 hr light/dark regime. A rope perch was attached diagonally across each cage and floors were lined with waxed paper to facilitate daily cleaning.

Before the experiment began all birds were examined, weighed, randomly ascribed to cages, and then left to condition for 3 d. Caged kestrels were each fed two day-old cockerel chicks per d at 0900 H each morning and uneaten food was removed at 1600 H. Cockerel chicks are the staple diet used throughout the McGill colony and kestrels fed *ad lib* normally eat 1–1.5 cockerels/d. After the conditioning period, the kestrels were fasted for 1 d before each experiment was begun.

Mason et al. (1991) report that isomers of aminoacetophenone are at least an order of magnitude more repellent to European Starlings than is methyl anthranilate. Therefore, 1% (m/m) 4-aminoacetophenone and 10% (m/m) methyl anthranilate in 85% ethanol were chosen for investigation. Test food was prepared daily by spraying cockerel chicks with one of these solutions until all the

perinatal down was saturated, or with 85% ethanol only in the case of controls. The ethanol was then allowed to evaporate for 1 hr before the chicks were packaged and stored under refrigeration. Treated chicks and controls were visually indistinguishable to human experimenters. However, cockerels were discretely labelled by amputation of distal toes and half of the lower mandible. This label was randomly alternated between test and control cockerels for each d of the food choice experiments.

Two variables were scored in the feeding trials. One of these was "first choice" (i.e., the cockerel which a kestrel moved directly to and took hold of from perching). In the test situation this is not necessarily the food item which the kestrel eventually consumed but was considered analogous to a wild kestrel perch-hunting, the species' most frequent hunting technique (Bildstein and Collopy 1987, Varland and Klaas 1991). The second variable scored was the amount of food eaten by each kestrel between 0900–1600 H each day.

It is difficult to measure quantitatively the amounts of cockerels consumed by caged kestrels. After thawing, water evaporates from partly consumed cockerels, which usually also become contaminated with kestrel feces. Therefore, taking fresh weights of intact cockerels and leftovers is not a reliable way of calculating food consumed. However, cockerels are remarkably constant in size; mean fresh mass in this study was 41.04 ± 0.61 g, (CV = 0.87%, $N = 30$). This remains so for the proportions of their body parts. The head and neck is 0.17 of a whole cockerel, eviscerated torso 0.40, yolk sac 0.16, other viscera 0.09, each pectoral limb 0.02, thighs 0.06, and feet 0.01 each. Food consumption could, therefore, be accurately assessed as proportions of "day-old cockerel units." When feeding, kestrels sometimes first plucked some of the perinatal down from a cockerel and then began eating the head. It is possible that in this way they avoided ingesting chemical additives.

Experiment 1. Kestrels were divided randomly into three groups of 11 birds each. No significant differences between groups was found for the body mass of the kestrels ($\bar{x} = 113.71 \pm 0.46$ g, $N = 33$, CV = 6.02%). The first group of 11 was used to test the reaction to food treated with methyl anthranilate, a second the reaction to food treated with 4-aminoacetophenone, and the final control group assessing voluntary food intake.

A two-choice experimental procedure (Mason et al. 1989) was followed for the first two groups. Kestrels were given a choice of one treated (treated with either repellent) and one untreated day-old cockerel, each day for 4 d. Each day at 0900 H, the two cockerels were placed in each cage, and within approximately 15 min after food introduction the first choice selection by the kestrels was recorded. At 1600 H, food remains were removed and assessed to determine the amount of food consumed in "day-old cockerel units." Kestrels in the control group were each fed daily with two control cockerels and food consumption similarly measured. On day 5, all birds were reweighed, given two untreated cockerels each and the opportunity to bathe. Total food consumed was measured for each bird at the usual time.

Experiment 2. In nature, predators may learn to avoid unpalatable prey animals which are aposematically (warningly) colored (Mathews 1977, Turner 1977), some even

Table 1. Numbers of kestrels in methyl anthranilate treated group ($N = 11$) and 4-aminoacetophenone treated group ($N = 11$) choosing treated day-old cockerels for days 1–4 ($n = 11$). P -values refer to significance of a χ^2 test with $df = 1$.

TREATMENT	DAY 1		DAY 2		DAY 3		DAY 4	
	NUMBER	P	NUMBER	P	NUMBER	P	NUMBER	P
Methyl anthranilate group								
With methyl anthranilate	4		1		2		4	
Untreated	7	0.104	10	0.007	9	0.035	7	0.336
4-aminoacetophenone group								
With 4-aminoacetophenone	6		2		6		4	
Untreated	5	0.763	9	0.035	5	0.763	7	0.336

possessing an innate ability to avoid certain colors (Lindstrom et al. 1999). The second experiment tested whether aversive conditioning in kestrels is facilitated by linking an unfamiliar color to a potentially aversive chemical. In this experiment, 10% 4-aminoacetophenone, which was 10 times the concentration used in Experiment 1, was used. This higher concentration was chosen in order to give the maximum likelihood of achieving a conditioned response to the chemical additive. Day-old cockerels are usually pale yellow and this color was masked by adding green or blue food dyes to the ethanol mixture sprayed onto them.

Kestrels from Experiment 1 were rested and well fed for 1 week in large flight cages. Twenty-two kestrels from the first experiment and 11 additional kestrels were then weighed and reintroduced to test cages and ascribed to three random groups as in Experiment 1. Cross-sampling assured that kestrels exposed to a particular chemical in the first experiment were not in the second. After a 1 d fasting, they were offered four day-old cockerels each day for 3 d according to one of the following three regimes: (1) Control group—two cockerels dyed with green (green control) and two dyed with blue (blue control) food coloring; (2) Green + 4-aminoacetophenone group—two cockerels dyed green then treated with 10% 4-aminoacetophenone (green + 4-aminoacetophenone) and two dyed blue (untreated blue); (3) Blue + 4-aminoacetophenone group—two cockerels dyed green (untreated green group) and two dyed blue then treated with 10% 4-aminoacetophenone (blue + 4-aminoacetophenone group). First choice and total food consumed was measured each day as in Experiment 1 and kestrels were re-weighed after 4 d.

A further experiment showed that kestrels did not discriminate between undyed cockerels and those dyed with yellow food color.

RESULTS

Experiment 1. Significantly more (χ^2 test, $df = 1$) kestrels chose untreated day-old cockerels on day 2 for both the methyl anthranilate ($P = 0.007$) and 4-aminoacetophenone ($P = 0.03$) groups and also on day 3 for methyl anthranilate ($P = 0.03$; Table 1). On day 1 and 4, treated and untreated

cockerels were chosen at random and there was no significant differences in the number of kestrels choosing the two types of food.

Although it seemed that kestrels ate more untreated than treated food, treated food is also eaten, apparently peaking on day 3 for both treatment groups (Fig. 1). There was no evidence of vomiting caused by ingestion of treated food. What is clear, however, was that total food consumed by kestrels in the treatment groups tracked closely that voluntarily consumed by the control group. Had the chemical additives deterred kestrels from eating treated food, then it might have been expected that total food consumption by treatment kestrels would have been less than for controls. Analysis of variance showed this to be the case ($P = 0.0$ for treatment effect, repeated measures analysis of variance with $df = 2,115$) with rank order of food consumed in the sequence: control group > methyl anthranilate treatment group > 4-aminoacetophenone treatment group.

Presumably, the lower rates of food consumption of test groups was caused by kestrels avoiding treated food and so limiting their food intake. Paired t -tests confirmed this to be so (Table 2), however, no significant difference (ANOVA, $P = 0.901$, $df = 2,29$) in body mass between the three groups could be detected at the end of the trial on day 5. It seemed, therefore, that although kestrels in the treatment groups limit their food intake, they did not completely avoid treated food (Fig. 1) nor compromise their body reserves. Further comparison of post-test (day 5) intake of untreated day-old cockerels showed no difference between treatment groups and controls (ANOVA, $P = 0.199$; $df = 2,28$; 2 missing data items). These results together suggested that although the two test chemicals

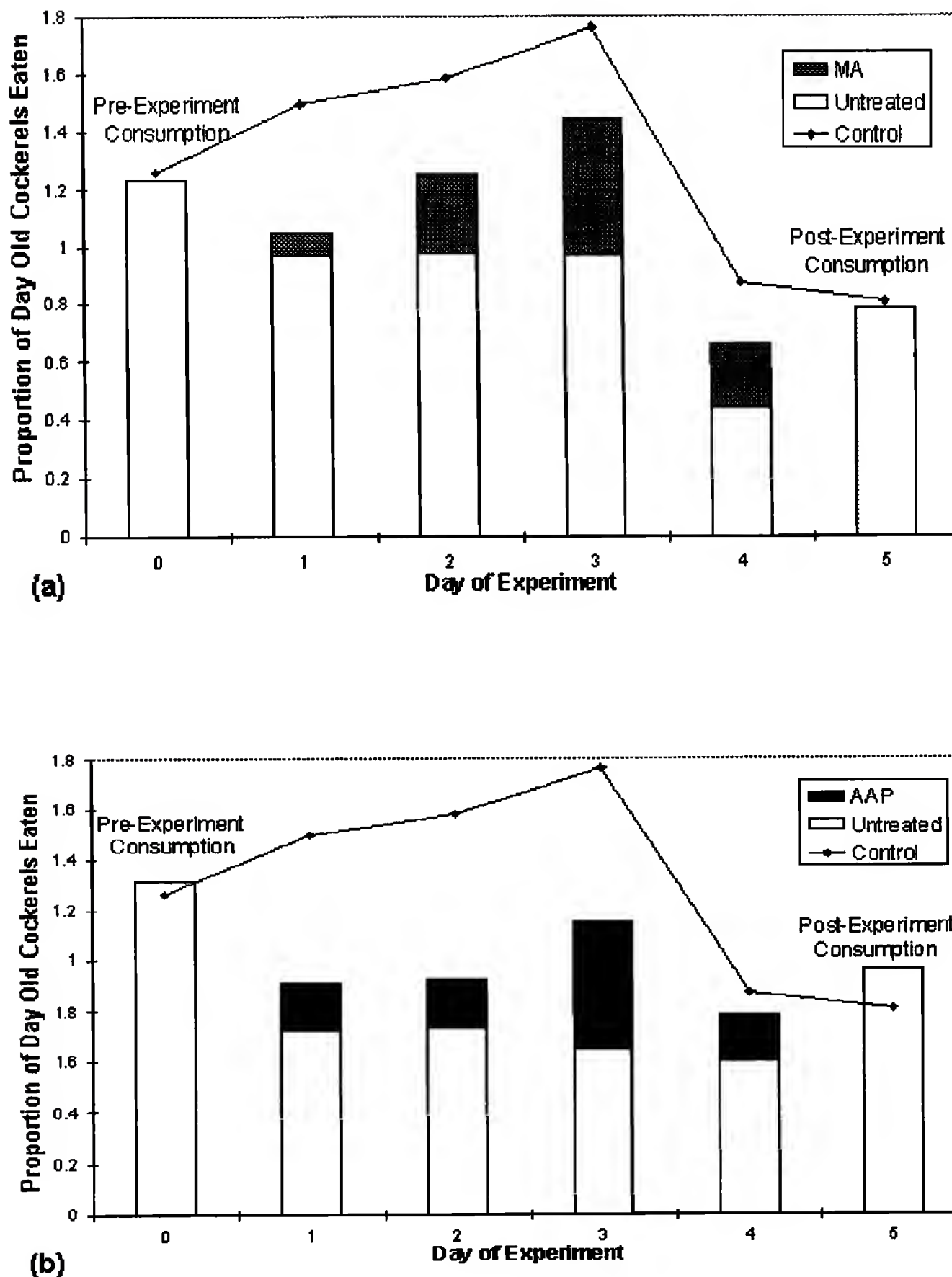


Figure 1. Consumption data for American Kestrels ($N = 11$) in (a) the methyl anthranilate treated group and (b) the 4-aminoacetophenone treated group compared with voluntary food intake of control groups ($N = 11$).

were at least avoided, 4-aminoacetophenone more so than methyl anthranilate, they were not truly aversive. Aversive chemicals would cause kestrels to avoid a particular food type even at the expense of compromising basal energy requirements and further cause them to avoid eating that food type even after chemical treatment had ceased.

Experiment 2. Only green- and no blue-colored

day-old cockerels were consumed during the experiment. All but two kestrels chose green cockerels as their first choice in all groups; the remaining two birds chose not to eat at all. The green cockerels eaten by kestrels in the control and blue + 4-aminoacetophenone groups were all untreated; effectively, therefore, this second group acted as a further control. Moreover, kestrels in the

Table 2. Summary of a series of paired *t*-tests (each with *df* = 10) comparing consumption of methyl anthranilate treated *vs.* untreated and 4-aminoacetophenone treated *vs.* untreated food by American Kestrels. *N* = 11 kestrels in each treatment group and, where significant differences were found, the mean consumption of untreated food was greater than that of the treated food.

TREATMENT	DAY 1		DAY 2		DAY 3		DAY 4	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Methyl anthranilate treated <i>vs.</i> untreated food	33.39	0.0	7.1	0.0	3.78	0.0036	1.04	0.32*
4-aminoacetophenone treated <i>vs.</i> untreated food	3.92	0.003	3.27	0.009	0.65	0.53*	2.99	0.014

* Not significant.

green + 4-aminoacetophenone group preferred to eat 4-aminoacetophenone treated green cockerels rather than untreated blue cockerels (Fig. 2). Although there was a trend (control group > blue + 4-aminoacetophenone group > green + 4-aminoacetophenone group) in the total amount of food consumed, analysis of variance showed this as not significant (*P* = 0.35, *df* = 2,29). In all cases, however, food intake was very low, averaging less than 0.5 day-old cockerels per kestrel per d, and, as mentioned, some kestrels refused to eat during the entire experimental period. Although most

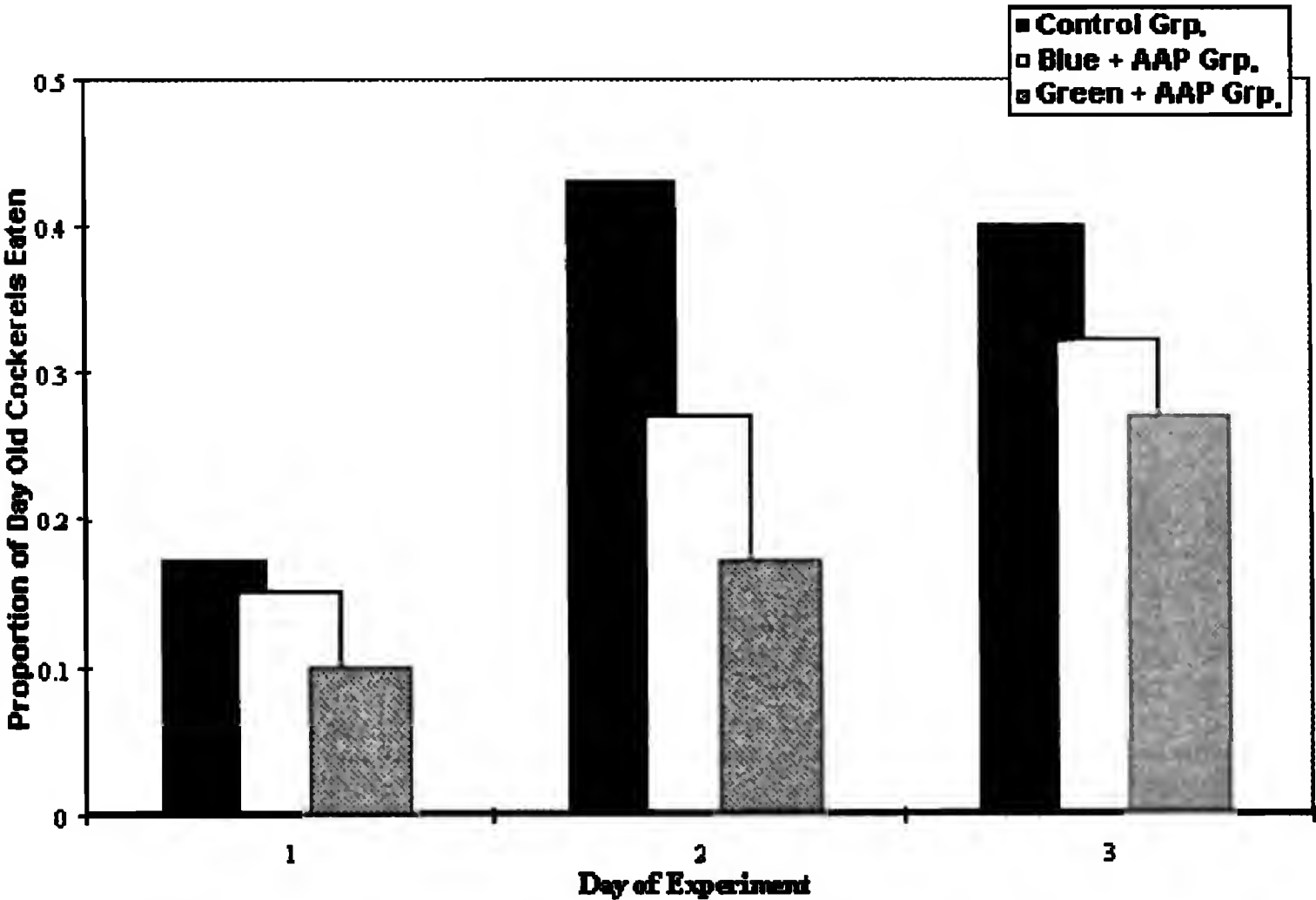


Figure 2. Comparison of total amounts of green-dyed day-old cockerels consumed by American Kestrels in Experiment 2. Treatment 1—control group or kestrels offered untreated green and blue day-old cockerels; treatment 2—blue + 4-aminoacetophenone group or kestrels offered untreated green and blue day-old cockerels and day-old cockerels treated with 4-aminoacetophenone; and treatment 3—green + 4-aminoacetophenone group or kestrels offered untreated blue and green day-old cockerels and day-old cockerels treated with 4-aminoacetophenone. In no case were blue-dyed day-old cockerels eaten.

kestrels lost weight during the trial, no significant differences in the amount of weight loss could be found by analysis of variance ($P = 0.54$, $df = 2,29$). Because food intake was low throughout and to avoid fatality due to starvation, the experiment was terminated after 3 d.

DISCUSSION

The use of deterrent feeding chemicals may be loosely divided into those which cause food to be unpalatable, can be detected by the predator either directly or by associated visual cues and so emulate aposematic protection, and those tasteless substances which cause feelings of sickness and so evoke a conditioned taste aversion response to a particular food (Clark 1997, Reynolds 1999).

Kestrels in our experiments seemed to be able to discriminate and avoid day-old cockerels treated topically with 4-aminoacetophenone and methyl anthranilate when they were novel. However, in the absence of alternate adequate food, kestrels ate cockerels treated with these chemicals, presumably to maintain their caloric needs. There was, therefore, no evidence to suggest that kestrels were prepared to starve and so compromise body condition. As a contrast, McKay et al. (1999) showed that lasting aversion to dead trout could be conditioned in cormorants (*Phalacrocorax carbo*) fed previously on trout treated with carbochal. Although Musgrove (1997) showed that methyl anthranilate mixed into chopped meat caused vomiting in large falcons, we found no evidence of such violent reaction in kestrels where methyl anthranilate and 4-aminoacetophenone was applied topically to food. Both chemicals seemed, therefore, to be unpalatable rather than truly aversive to kestrels and so a conditioned taste aversion response did not seem possible.

Interestingly, the kestrels' aversion to unfamiliar color, particularly blue, was stronger than that to the chemical additives. The test kestrels are familiar solely to food of one type, yellow day-old cockerels. Blue-dyed cockerels were such a deterrent to some kestrels that, rather than eat them, they preferred food treated with 4-aminoacetophenone. Further, although they would eat green-dyed cockerels, their food intake was low. It seemed, therefore, that unfamiliar color, and not the chemicals, was a more aversive agent.

It may be said that these domestic kestrels feeding on dead cockerels are not a proper test of wild circumstances. However, the findings in our study

appear to be compatible with previous studies on captive kestrels and analogous to studies on wild kestrels and the innate avoidance of certain colors by other predators (Lindstrom et al. 1999). In laboratory studies, Mueller (1987) showed that while American Kestrels developed long-term preferences for particular types of prey, they would still sample novel prey if it was still within the limits of what occurred in nature. He further inferred from the literature on laboratory and field studies that such specific search images are also formed by free-ranging kestrels and other birds of prey.

A more serious consideration is whether predatory birds conditioned to avoid dead prey, would transfer that avoidance behavior to live alternatives. Whether kestrels conditioned to avoid dead cockerels will transfer this behavior to live prey needs further study. It may, however, be feasible to condition free-living raptors to avoid a potential prey by treating live prey with chemical deterrents. It is reasonable to assume that in a field application with ample alternative prey available, the application of methyl anthranilate and 4-aminoacetophenone, or indeed some other proven agent, to a group of potential prey animals may condition a response in the predator causing it to avoid the treated group and hunt elsewhere. However, as our results suggest, if prey abundance is locally limiting and no alternative available, then treatment of prey with methyl anthranilate or 4-aminoacetophenone, at least at the concentrations tested nor higher concentrations, is not likely to deter predation. Methyl anthranilate is an oily liquid at normal temperatures and 4-aminoacetophenone a crystalline solid. Both chemicals were tested at what appeared to be maximum possible levels (10% m/m), but consumption of treated food by kestrels still occurred. Higher levels applied to, say, game birds or pigeons in the field may cause impairment of feather maintenance, increased time spent preening, and possibly increased vulnerability to factors such as cold or wet weather. Research into the repercussions of the chemicals applied to the plumage of the prey animals they are meant to protect would have to be undertaken. Perhaps, an alternate solution would be to feed potential prey items chemicals which would render their flesh unpalatable to their avian predators, emulating more closely naturally unpalatable and therefore protected animals. In addition, it may even be more efficient to use visual cues such as sufficiently novel colors, rather than chemicals, to at least initially

deter raptors from taking prey of human economic importance. However, the degree to which a color remains novel to a particular predator in wild circumstances is a complicated question (see Allen and Clarke 1968).

Given that the use of dead baits poses problems of transference of avoidance to live prey, this raises an important question concerning in what situations, if any, such management practices would best be aimed. The chemical protection of wild adult prey would not be feasible due to the difficulty and cost of catching them and then applying a sufficient amount of the deterrent chemicals. A more practical application of chemical deterrents may be their use in the protection of game bird young at wild release sites or domestic homing pigeons associated with a particular home loft. Protection from a single, attentive raptor, in these circumstances, could possibly be insured by the combination of an aversive chemical and associated aposmatic visual cues.

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SHORT COMMUNICATIONS

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RESPONSIVENESS OF NESTING EURASIAN KESTRELS *FALCO TINNUNCULUS* TO CALL PLAYBACKS

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KEY WORDS: *Eurasian Kestrel*; *Falco tinnunculus*; *playback*; *nesting period*; *survey technique*.

Many birds of prey, both diurnal and nocturnal, respond to playback of their own calls (Fuller and Mosher 1981, Morrell et al. 1991, Cerasoli and Penteriani 1992, Redpath 1994). This responsiveness has led to the development of acoustic methods for detecting and counting raptors, particularly in woodland habitats (e.g., Mosher et al. 1990, Cerasoli and Penteriani 1992). By contrast, diurnal raptors found in open habitats are seldom surveyed using taped broadcasts because they are easily detected by observers. Nevertheless, difficulties in locating these raptors can arise, especially when there is a mosaic of habitat types across the landscape or when the architectural complexity of old buildings and ruins in urban areas supplies additional nest sites. The aim of this study was to assess the response of breeding pairs of Eurasian Kestrels (*Falco tinnunculus*), which can be widespread in European urban areas (Village 1990), to the playback of their calls in order to evaluate the efficiency of this method for surveying for nests of this species.

METHODS

The study was carried out on the Eurasian Kestrel population that nests in scaffolding holes of Roman ruins and old buildings in the center of Rome, Italy. This population has been studied since 1995 and has shown a very high breeding density (Piattella et al. 1999). During April–June 1998, 36 taped broadcast sessions were performed at 20 known occupied nests. Nine sessions were performed in April, 16 in May, and 11 in June. To avoid habituation to playback and disturbance during the breeding season, breeding pairs were not tested more than twice (e.g., Redpath 1994) during the entire study period.

Playbacks were performed at each occupied nest in early morning (0700–1000 H, $N = 13$ playback sessions),

late morning (1000–1300 H, $N = 9$), early afternoon (1300–1600 H, $N = 7$), and late afternoon (1600–1900 H, $N = 7$). Signal calls, a series of high-pitched trills especially uttered by females denoting the presence of breeding pairs near nests (Village 1990), were used for eliciting responses of kestrels. Each playback session was conducted giving five taped calls lasting approximately 1 min at 2-min intervals. Taped broadcasts were performed using a portable stereo with 6 W amplifiers. Taped calls were stopped once a bird responded (latency time). Broadcast points were located in the streets around buildings used by breeding pairs of kestrels, at a minimum distance ranging 30–40 m. During each playback session, each of the following were recorded: the date and time of stimulation, minimum daily temperature and wind speed (values obtained from the meteorological station of "Ufficio Centrale di Ecologia Agraria" in the city center), latency (time from start of broadcast to first response), sex of the responding individual, and response type classified as (1) appearance of a kestrel at the nest entrance, (2) advertising or alarm calls, (Village 1990), (3) flights around the nest site (taking into account only individuals flying away from nest entrances or from perches close to nest holes), (4) copulation near nests, (5) no response, and (6) behavior of young (only for nests completely visible by the observer). Nearest-neighbor distance (nnd) was also calculated including all breeding pairs, even those not tested by playbacks.

Breeding pairs were located in the study area (about 10 km²) by visiting known nest sites and checking other suitable nest sites with standard census methods (Village 1990). Breeding success was determined by checking nest sites at least twice and counting all visible fledglings. Nests where complete counts of fledglings could not be made were not included in the analysis.

Percentages of successful playbacks were calculated with reference to the number of playbacks performed in each month and over the study period, respectively. In calculating percentages of successful playbacks, we regarded as successful each playback that caused any type

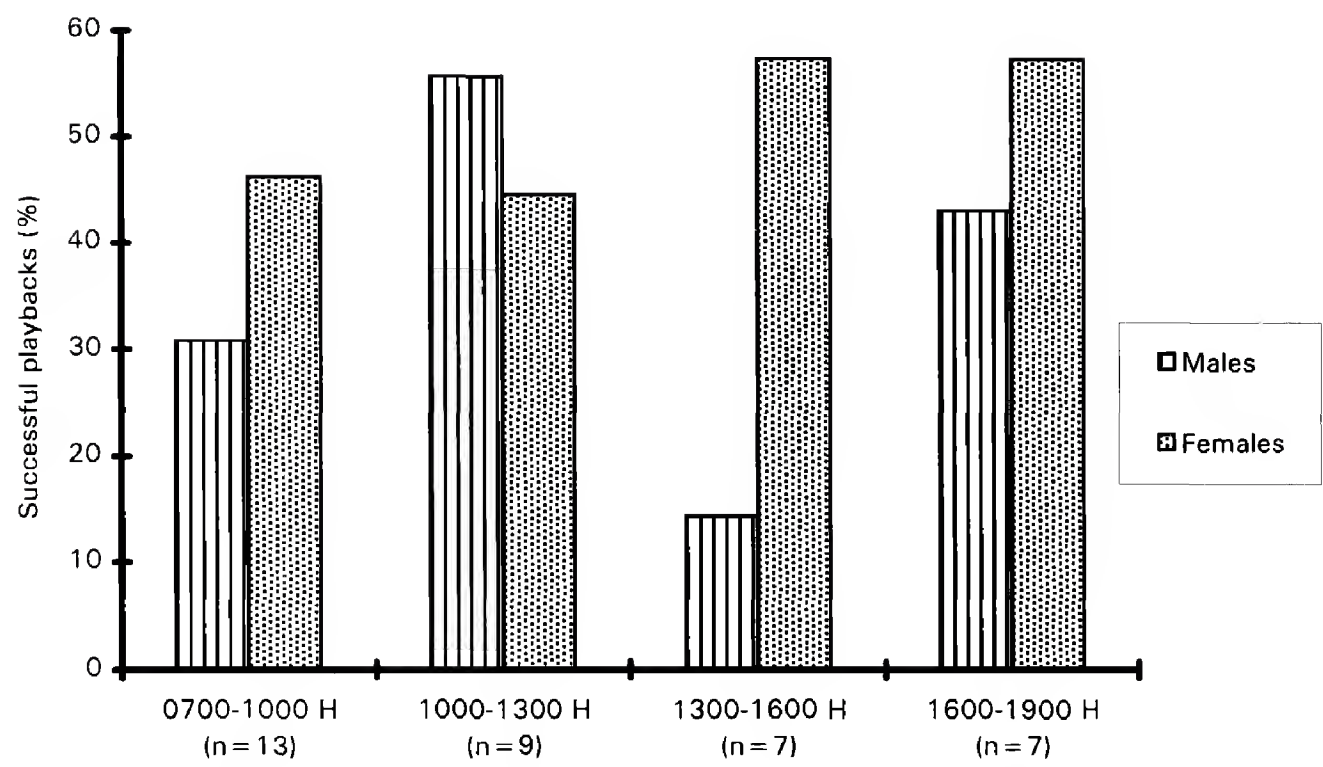


Figure 1. Daily response pattern of breeding Eurasian Kestrels to taped broadcasts.

of response by males, females or both together. Also, we calculated separately the percentages of males and females that responded to playbacks in each month for the total playbacks performed in each month. Finally, a “response index” indicating the intensity of responses was calculated for each pair by summing of all response types of the male and female (giving the value 1 to all positive types of responses) and dividing it by the total number of playbacks. Values of response time and response index recorded for each pair were compared to date, time of stimulation, temperature, wind, nearest-neighbor distance, and breeding success using the Spearman rank correlation tests. Differences between female and male latency were tested by using Mann-Whitney *U*-test (*U*-value corrected to a *z* score). All tests were two-tailed and $\alpha = 0.05$.

Table 1. Responses of breeding Eurasian Kestrels to call playbacks in Rome, Italy. Total responses, appearances, vocalizations, and flights are expressed for each sex as number of observed events and percentages on both sexes. Percentage of copulations is calculated for the total number of taped broadcast stimulations. Response time, as well as response index, are expressed as $\bar{x} \pm \text{SD}$.

	FEMALES	MALES	N
Response time(s)	17 ± 28	65 ± 108	36
Total responses	18 (58.1%)	13 (41.9%)	31
Appearances	16 (72.7%)	6 (27.3%)	22
Vocalizations	9 (50.0%)	9 (50.0%)	18
Flights	3 (23.1%)	10 (76.9%)	13
Copulations	4 (11.1%)		36
Response index	2.2 ± 1.5		16

RESULTS

A total of 26 of 36 playbacks resulted in responses by kestrels. Eight (88.9%) of 9 playbacks performed in April, 10 (62.5%) of 16 playbacks performed in May, and 8 (72.7%) of 11 playbacks performed in June resulted in responses. Four playbacks (44.4%, *N* = 9) in April, 5 (31.3%, *N* = 16) in May, and 4 (36.4%, *N* = 11) in June resulted in responses by male kestrels. Seven playbacks (77.8%, *N* = 9) in April, 7 (43.8%, *N* = 16) in May, and 4 (36.4%, *N* = 11) in June resulted in responses by female kestrels. In some cases, males and females of the same pair responded together to the stimulation (Fig. 1, Table 1). Thus, the same playback could have produced a double response. Likewise, multiple types of behavioral reactions were sometimes elicited by a single stimulation. All the individuals responded within 5 min from the start of playbacks and the difference between male and female latency was not significant ($z = -1.06$, $P = 0.29$, *N* = 31). During incubation and brooding, females appeared at nest entrances and called regularly for about 1 min, but rarely flew from nests rapidly reentering nests after this display. Males seldom appeared at nest entrances throughout the study period. When males were inside nest-holes, they showed behaviors similar to those shown by females, appearing at nest entrances and excitedly calling, but rapidly reentering nest cavities. At all nests where young birds were observed, young kestrels never responded to taped calls. Instead, they always hid themselves in an internal corner of the hole during playbacks.

No significant correlations were found between response time and the following variables: date ($r_s = 0.28$, $P = 0.124$, *N* = 31), time ($r_s = 0.08$, $P = 0.663$, *N* = 31), temperature ($r_s = 0.32$, $P = 0.076$, *N* = 31), wind ($r_s = -0.02$, $P = 0.921$, *N* = 31), and *nnd* ($r_s = -0.13$, $P = 0.480$,

$N = 31$), and breeding success ($r_s = 0.29$, $P = 0.205$, $N = 21$). Likewise, no significant correlation was found between these variables and the response index: $r_s = -0.17$, $P = 0.349$, $N = 31$ for date; $r_s = -0.24$, $P = 0.184$, $N = 31$ for time; $r_s = -0.18$, $P = 0.326$, $N = 31$ for temperature; $r_s = 0.16$, $P = 0.384$, $N = 31$ for wind; $r_s = 0.04$, $P = 0.829$, $N = 31$ for nnd; or $r_s = -0.30$, $P = 0.185$, $N = 21$ for breeding success.

For a total of 20 nesting pairs, occupation of 16 nest sites (80%) was directly confirmed by playback stimulation.

DISCUSSION

The broadcasting of taped calls is a useful tool in locating nesting raptors in woodland settings (Fuller and Mosher 1981). The technique used in this study may represent a first time such a technique has been used to detect nesting pairs of nonforest species. We found that, after occupation, both male and female kestrels defended nest sites from neighboring and intruding kestrels. Because of this, vocalizations of breeding kestrels could be easily elicited by broadcasting a taped call, such as the "signal call," especially in the first stages of the nesting period. Although kestrels are not highly territorial (Village 1990), their response to playbacks was relatively high compared to other diurnal raptors (Mosher et al. 1990, Cerasoli and Penteriani 1992), indicating that the playback method may integrate other field techniques in locating breeding pairs of Eurasian Kestrel. The playback method may be particularly useful in high density populations where observers must check the occupation of two or more neighboring nest sites. As kestrels are very versatile in their choice of nest sites and their identification can be very difficult (Shrubb 1993), this technique may also be a practical tool in low density situations. For example, in cases where kestrels have a scattered distribution, this technique can be used to cover relatively large areas in a short time and it is a faster method of surveying for kestrels when they nest in uncommon sites and habitats (e.g., crow nests in pine plantations). Nevertheless, because playback methods are invasive, researches should minimize disturbance to the pairs studied by performing playbacks only in the first stage of the breeding season and each nest should not be visited more than twice during the breeding season. Finally, playbacks should not be used in counting fledglings because they do not respond to playbacks and seem to be disturbed when adults respond to calls.

RESÚMEN.—La respuesta de parejas de *Falco tinnunculus* a las vocalizaciones grabadas fue estudiada en una población urbana en Roma, Italia. Los Cernícalos respondieron con varios despliegues cerca de sus nidos. La eficiencia de los "playbacks" y la latencia individual fueron similares entre machos y hembras. No hubo una correlación entre las tasas de respuestas y el clima, o entre las variables de población. Los "playbacks" pueden aumentar el número de técnicas de campo para la localización de parejas en reproducción.

[Traducción de César Márquez]

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THE BREEDING SUCCESS OF TAWNY OWLS (*STRIX ALUCO*) IN A MEDITERRANEAN AREA: A LONG-TERM STUDY IN URBAN ROME

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KEY WORDS: *Tawny Owl; Strix aluco; breeding success; annual fluctuations; Mediterranean areas; urban Rome.*

The breeding biology of the Tawny Owl (*Strix aluco*) was studied in northern and central Europe specifically focusing on the influence of food abundance on clutch size and productivity of young (Southern 1970, Wendland 1984). Baudvin (1990) found a remarkable positive correlation between the reproductive output of Tawny Owls and the percentage of woodland rodents in the diet of pairs in central France. Annual fluctuations in Tawny Owl breeding success were directly linked to the abundance of woodland rodents, especially the yellow-necked mouse (*Apodemus flavicollis*), the main prey of this owl in woods and mixed farmlands (Wendland 1984, Baudvin 1990, Jedrzejewski et al. 1994). Moreover, alternative prey (e.g., birds and amphibians) increased in diet in low mouse years (Plesnik and Dusik 1994). Cyclic fluctuations in populations of rodent prey is probably the main factor affecting Tawny Owl productivity, but other factors, such as weather conditions, could be also involved (Kostrzewa and Kostrzewa 1990, Gil-Delgado et al. 1995, Penteriani 1997).

In Mediterranean areas, very few studies have focused on the study the annual variations in the breeding success of any raptor (Gil-Delgado et al. 1995). The aim of this study was to assess the long-term breeding success of Tawny Owls in a Mediterranean urban area, checking for variations, if any, in productivity of young, and comparing them to the breeding performance of other areas in Europe.

METHODS

The study was carried out from 1984–99 in five urban census plots, including developed areas, small gardens, and city parks (mean density of Tawny Owl territories = 3.0/km²) and from 1989–99 in three suburban plots of Rome, including open land and deciduous woodland patches (mean density of Tawny Owl territories = 5.6/km², Ranazzi et al. 2000). Vegetation in small gardens included pines (*Pinus pinea*), cypresses (*Cupressus sempervirens*), cedars (*Cedrus* spp.), as well as isolated oaks (*Quer-*

cus spp.). Vegetation of city parks as well as suburban woodlands was generally composed of strands of mixed deciduous wood predominated by oaks (e.g., *Quercus ilex*). Nests were generally located in natural cavities of old oaks and pines. The rate of territory occupation was remarkably high in both habitats, so the population density did not show significant variations among years (Ranazzi et al. 2000).

Procedures for mapping territories and locating nesting sites followed Ranazzi et al. (2000). Although the bulk of the data on breeding success were obtained from pairs consecutively studied throughout the census period, some pairs, especially those of urban parks, were not continuously censused due to the impossibility to visit their territories in some breeding seasons (e.g., occurrence of summer events or public works in parks and gardens and Tawny Owls nesting sometimes on private property). Data for 1984–85 seasons were not considered due to the small number of records available. The number of occupied territories censused each year was 14.3 ± 5.9 ($N = 200$) from 1986–99 in urban plots, and 10.1 ± 5.8 ($N = 111$) from 1989–99 in suburban plots.

Estimates of the number of young in nests were made by broadcasting calls of male Tawny Owls on a SANYO portable stereo with 6 W loudspeakers within the nesting area at a distance of about 50 m from known nest sites (see Ranazzi et al. 2000 for details) and listening for responses. Generally all young responded to calls with their persistent 'ptziè' begging calls, so this method was used to evaluate the number of successful pairs and fledgling production (Wendland 1984). Nest site disturbance was reduced by limiting visits to each territory to only two in May–August. This period was chosen to census young based on a preliminary assessment in 1984–85 of young vocal activity at eight known nests. All fledglings began to utter the 'ptziè' call in May and they remained in their parents' territories at least until early August, continuously uttering their begging calls. These data were consistent to those in non-Mediterranean zones (Southern 1970, Wendland 1984). Data gathered in early May or in August were included only if a control visit was made in June or July. When we were uncertain of the exact number of young that begged due to the many calls contemporaneously uttered, we omitted them from analyses.

We agree with Wendland (1984) that this method can

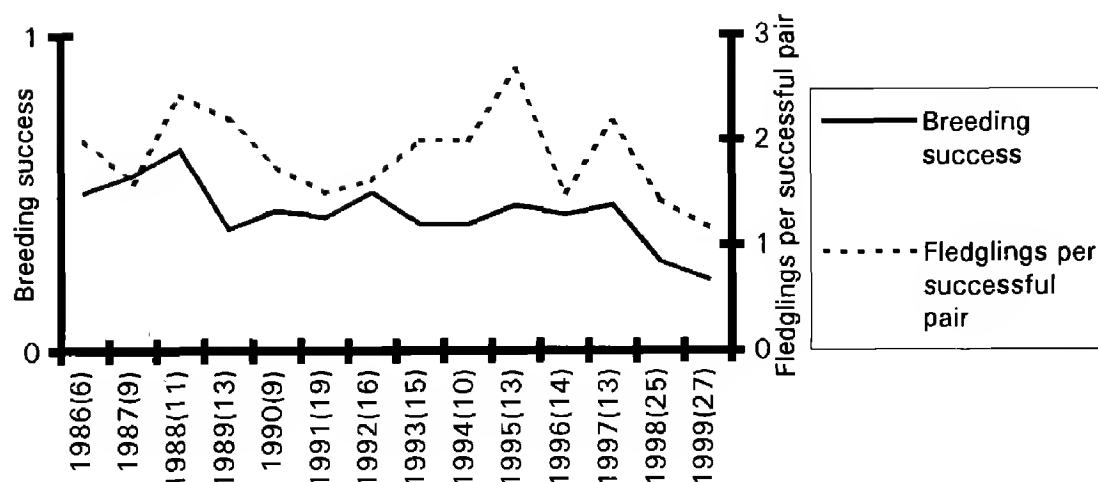


Figure 1. Annual variations in the rate of breeding success and mean number of fledglings per successful pair in urban Rome. Number of breeding attempts studied are given in parentheses.

result in small errors, but it allows checking of young in many natural cavity nests in a relatively short time. The breeding success was assessed using the following indexes: (1) breeding success (at least one young fledged); (2) number of fledglings per successful pair; and (3) number of fledglings per breeding pair. All data are presented as mean \pm SD. Meteorological data were acquired from a weather station within the study area. The rate of breeding success was compared by χ^2 contingency tables including numbers of successful and failed pairs. Parametric tests were used when data showed a normal frequency distribution. Comparisons between different habitats or study areas were generally performed by Student's *t*-tests and one-way ANOVAs using yearly means and SDs. For some bibliographic data sets, only means were available, so we could not test for differences among years. A minimum probability level of $P < 0.05$ was accepted and all tests were two-tailed. Statistical analyses were performed by STATISTICA 4.5 and PRIMER 1.0 PC packages.

RESULTS

Out of a total of 311 breeding attempts studied from 1986–99, in urban plots 119 (59.5%, $N = 200$) failed, 37 (18.5%) produced 1 fledgling, 24 (12.0%) produced 2 fledglings, 16 (8.0%) produced 3 fledglings, and 4 (2.0%) produced 4 fledglings. In suburban plots, 57

breeding attempts (51.3%, $N = 111$) failed, 26 (23.4%) produced 1 fledgling, 20 (18.0%) produced 2 fledglings, and 8 (7.2%) produced 3 fledglings. No significant differences in any breeding parameters were found among years in both urban (breeding success: $\chi^2 = 9.9$, $df = 13$, $P = 0.703$; mean number of fledglings per successful pair: $F_{13,67} = 1.4$, $P = 0.177$; and mean number of fledglings per breeding pair: $F_{13,186} = 1.5$, $P = 0.126$; Fig. 1) and suburban plots (breeding success: $\chi^2 = 9.3$, $df = 10$, $P = 0.501$; mean number of fledglings per successful pair: $F_{10,43} = 1.4$, $P = 0.177$; and mean number of fledglings per breeding pair: $F_{10,100} = 0.8$, $P = 0.636$; Fig. 2). Differences in breeding parameters between the two habitats studied were also not significant (breeding success: $\chi^2 = 1.6$, $df = 1$, $P = 0.204$; mean number of fledglings per successful pair: $t_{23} = 1.4$, $P = 0.187$; and mean number of fledglings per breeding pair: $t_{23} = 0.1$, $P = 0.937$). The mean number of fledglings per breeding pair recorded in suburban plots of Rome was comparable to those observed in similar habitats of Berlin Grunewald ($t_{30} = 0.7$, $P = 0.464$) and Oxford Wytham Wood ($t_{22} = 0.5$, $P = 0.597$), but lower than those observed in mixed woodlands of Cote d'Or ($t_{19} = 5.1$, $P < 0.001$) and farmlands of Hradec Kralowe ($t_{13} = 6.6$, $P < 0.001$), where

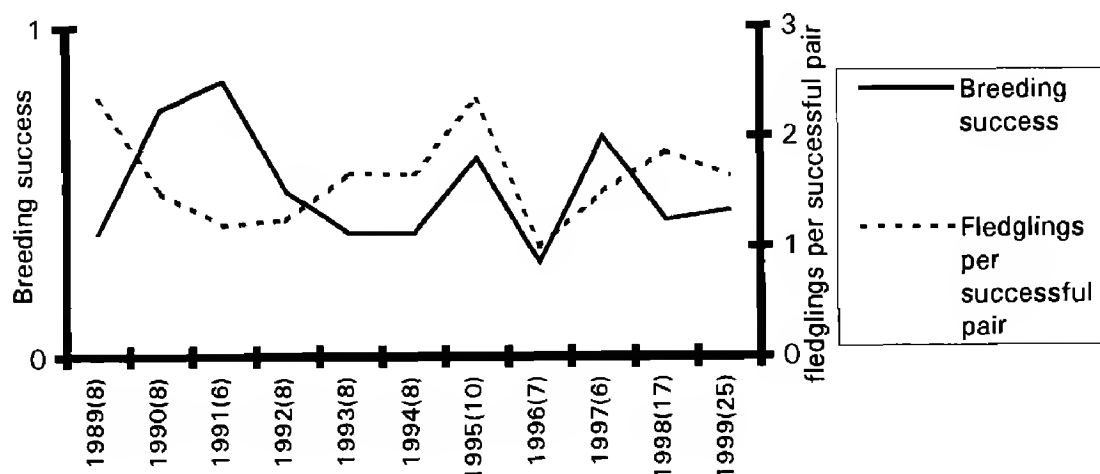


Figure 2. Annual variations in the rate of breeding success and mean number of fledglings per successful pair in suburban Rome. The number of breeding attempts studied are given in parentheses.

all Tawny Owl pairs bred in nest boxes. In northern European areas (see Table 1 for statistics and references), significant differences among years in the rate of breeding success were observed over a long-term period in both Berlin ($\chi^2 = 1382.9$, $df = 20$, $P < 0.001$) and Oxford ($\chi^2 = 57.2$, $df = 12$, $P < 0.001$), but no differences were observed in Cote d'Or ($\chi^2 = 11.7$, $df = 9$, $P = 0.233$) and Hradec Kralowe ($\chi^2 = 7.7$, $df = 3$, $P = 0.068$), probably due to the limited number of study years. As for the productivity of owl pairs, we could test for differences among years only in two areas, Hradec Kralowe and Kielder. In Kielder, the mean number of fledglings per breeding pair showed a significant difference among years ($t_{148} = 4.4$, $P < 0.001$). In Hradec Kralowe, the difference in productivity among years was not significant ($t_{80} = 0.9$, $P = 0.350$), again probably due to the small sample considered ($N = 183$ breeding attempts observed during four consecutive years).

DISCUSSION

The breeding success of Tawny Owls in Rome showed weak annual fluctuations when compared with those of some northern populations, although the overall production of young did not vary significantly among different populations nesting in natural cavities. In northern Europe, significant fluctuations in breeding parameters are specifically linked to the abundance of woodland rodents, which make up the main part of the Tawny Owl diet. In low rodent-years, breeding success is significantly lower than in high rodent years (Southern 1970, Wendland 1984, Petty 1989), and alternative prey, such as birds and amphibians, increase in the diet (Baudvin 1990, Plesnik and Dusik 1994). By contrast, as rodent fluctuations are weakly observed in Mediterranean areas (Rizzo et al. 1993, Gil-Delgado et al. 1995) and their abundance generally decreases along an urban gradient (Galeotti 1994), Tawny Owl reproduction in Rome should be less affected by this factor. In fact, in Mediterranean urban habitats as well as in most coastal and arid hilly areas, small mammals are a minor component of the diet which is composed mainly of birds and insects, especially beetles, as well as geckos, bats, frogs, and snails (Manganaro et al. 1999, Ranazzi et al. 2000). The availability of these prey throughout the breeding season (Capula et al. 1993, Rizzo et al. 1993, Gil-Delgado et al. 1995, Manganaro et al. 1999) allows Tawny Owls to avoid concentrating their predation on few mammal species, probably providing young with a comparable amount of prey each year. The use of alternative prey such as insects and stable breeding success have been observed in Mediterranean populations of the Eurasian Kestrel (*Falco tinnunculus*), a rodent-eating raptor that, in northern Europe, shows significant variations in its reproductive output due to cyclic fluctuations of its main prey (Rizzo et al. 1993, Gil-Delgado et al. 1995, Piattella et al. 1999). On the other hand, other factors affecting Tawny Owl reproductive output in northern Europe are probably reduced in southern Eu-

rope. Both harsh weather conditions and high levels of competition with other predators may increase fluctuations in population density as well as in reproductive output (Kostrzewa and Kostrzewa 1990, Selås 1998). In Rome, nighttime temperatures throughout the nesting season are generally higher than 10°C. From March–May 1984–98, the average temperature was $10.7 \pm 3.1^\circ\text{C}$ ($N = 15$ years), while during the post-fledging period, it was often higher than 20°C (average temperature in June 1984–98 = $17.9 \pm 1.2^\circ\text{C}$, $N = 15$ years). Also rainfall was generally low in both spring and early summer with rainfall in March–June 1984–98 averaging 189.9 ± 60.8 mm ($N = 15$ years). This provided good weather conditions for rearing young and reducing energy requirements when nestlings were growing (Gil-Delgado et al. 1995). As already observed for some raptors in cities (Sodhi et al. 1992, Tella et al. 1996), competition levels with other predators were substantially reduced in the study area, where only the Eurasian Kestrel, the Little Owl (*Athene noctua*), and the red fox (*Vulpes vulpes*) reached relatively high densities in some Tawny Owl habitats. Therefore, both mild weather conditions and low level of trophic competition with other predators may have further accounted for the long-term stability of the Tawny Owl breeding success in Rome.

RESÚMEN.—La reproducción de *Strix aluco* fue estudiada desde 1984–99 y en 1989–99 en la Roma urbana y sub-urbana respectivamente. El éxito de anidación y el número medio de pichones por parejas exitosas y por parejas en reproducción no tuvo variaciones significativas en un período de 15 y 11 años en habitats urbanos y suburbanos respectivamente. Comparado con las poblaciones del norte de Europa, los factores principales que afectan la estabilidad de la población reproductiva de *Strix aluco* en Roma pueden estar relacionados con la dependencia de roedores en bosques, los cuales tienen una disponibilidad limitada en las áreas urbanas mediterráneas. También es importante su alta dependencia de fuentes alternas de alimento, tales como aves y geckos. Las condiciones climáticas durante la primavera y el verano son favorables para la cría de juveniles, permitiendo una considerable reducción de energía requerida en la estación reproductiva. Existe también una limitada competencia por comida con otros depredadores.

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Table 1. Breeding success of some European populations of Tawny Owls.

STUDY AREA (HABITAT TYPE)	NEST TYPE	STUDY PERIOD (NO. YEARS)	BREEDING SUCCESS		FLEDGLINGS/ SUCCESSFUL PAIR		FLEDGLINGS/ BREEDING PAIR		NO. OF PAIRS	SOURCE
			MEAN ± SD (RANGE)	χ	MEAN ± SD (RANGE)	F	MEAN ± SD (RANGE)	F		
Rome (Urban)	C ^a	1986–99 (14)	43.5 ± 10.4 (22.2–63.6)	ns ^b	1.86 ± 0.42 (1.17–2.43)	ns	0.83 ± 0.32 (0.26–1.55)	ns	200	This work
Rome (Subur- ban)	C	1989–99 (11)	51.0 ± 17.7 (28.6–83.3)	ns	1.63 ± 0.42 (1.00–2.33)	ns	0.82 ± 0.30 (0.29–1.40)	ns	111	This work
Berlin (DW) ^a	C	1959–79 (21)	44.8 ± 16.3 (21.1–76.9)	*	1.99 ± 0.36 (1.25–2.60)	— ^c	0.93 ± 0.44 (0.40–1.77)	— ^c	368	Wendland (1984)
Oxford (DW)	B + C	1947–59 (13)	44.5 ± 20.9 (0–70.0)	*	1.48 ± 0.55 (0–2.0)	— ^c	0.74 ± 0.41 (0–1.3)	— ^c	331	Southern (1970)
Cote d’Or (DW)	B	1980–89 (10)	69.6 ± 10.0 (47.8–80.4)	ns	2.94 ± 0.74 (2.00–4.34)	— ^c	2.06 ± 0.75 (1.00–3.46)	— ^c	347	Baudvin (1990)
Hradec Kralowe (F)	B	1986–89 (4)	79.9 ± 10.1 (64.9–85.7)	ns	2.62 ± 0.40 (2.26–3.19)	— ^c	2.18 ± 0.49 (1.62–2.74)	ns ^d	183	Plesnik and Dusik (1994)
Kielder (CW)	B	1981–87 (7)	—	—	—	—	1.48 ± 1.2 ^e (0.20–2.58)	* ^d	210	Petty (1989)

^a DW = deciduous forest; CW = coniferous forest; F = farmland; B = nest box; C = natural cavity.

^b Probability levels for each statistical test reported as follows: ns = $P > 0.05$; * = $P < 0.001$.

^c Yearly means with SDs were not available, so we could not test for differences among years.

^d Differences between the mean number of fledglings in high compared to declining vole years.

^e Mean and SD calculated using the mean values of many different years pooled into three young production classes according to the relative abundance of rodents.

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NOCTURNAL ACTIVITY OF LESSER KESTRELS UNDER ARTIFICIAL LIGHTING CONDITIONS IN SEVILLE, SPAIN

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KEY WORDS: *Lesser Kestrel*; *Falco naumanni*; nocturnal activity; foraging behavior; prey deliveries.

Lesser Kestrels (*Falco naumanni*) are migratory, colonial small falcons. Kestrels in western European populations breed mainly in holes and crevices in large historic buildings within towns and villages, or often in abandoned farm houses scattered across the countryside (Cramp and Simmons 1980, González and Merino 1990, Negro 1997). The species is considered Endangered in western Europe (Biber 1994).

In the city of Seville in southern Spain, three Lesser Kestrel colonies remain in the downtown area. To our knowledge, no other city in western Europe as large as Seville (population 750 000) currently has Lesser Kestrel colonies. In Seville, the main colony of about 70 pr is located in the Cathedral. This Gothic building is the largest cathedral in Spain and third largest in the Christian world. One smaller colony is located in El Salvador (25 pr), a Baroque church nicknamed Seville's second cathedral located about 500 m away from the Cathedral itself, and another is at Montesión (7–10 pr), a small chapel about 1.5 km from the Cathedral (C. Melguizo and J.L. Ruiz unpubl. data). The size of the city's population of Lesser Kestrels has not changed significantly in the last 10 yr (J.J. Negro, C. Melguizo, and J.L. Ruiz unpubl. data), although the kestrels were surely more abundant in the past, when numerous breeding colonies thrived in different city buildings (González and Merino 1990).

Reports from the early 1970s (Andrada and Franco 1974) indicate that Lesser Kestrels were active at night around the Cathedral, where they apparently took advantage of the powerful ornamental illumination that highlighted this historic building. However, no systematic study was ever conducted to determine whether Lesser Kestrels were active at night on a regular basis at the Cathedral or at other locations in the city. The fraction of birds involved in nocturnal behavior was also unknown, although Andrada and Franco (1974) suggested that up to 50% of individuals in the Cathedral could be active on any given night. The goals of our work were to: (1) determine if Lesser Kestrels were active every night

under ornamental lights, (2) determine which fraction of the colony was active at night, (3) determine the function of nocturnal activity, and (4) describe this unusual behavior in a typically diurnal species. In addition, prey deliveries by adults were recorded at selected nests during day- and night-time hours to determine the relative contribution of nocturnal activities in raising nestlings.

METHODS

We monitored seven nests in the Cathedral, which were clustered in two groups of three and four nests, respectively. In El Salvador, where there is also ornamental illumination at night, we observed a group of five nests and a group of four nests. Nests within each group were close enough to permit simultaneous observation from vantage points in the street, at an average distance from the nests of about 40 m. Surveys were conducted on days 3, 11, 17, 20, and 21 June 1998, coincidental with the period when young were in nests. Focal nests were monitored with 10× binoculars and 20–60× spotting scopes during three time periods: midday (1200–1400 H), late afternoon (1800–2000 H), and night (2200–2400 H). The first two periods occurred during full daylight. Sunset took place at about 2130 H during the study period, and ornamental illumination was on between 2200–2400 H, coincidental with our nighttime observations. Total observation time amounted to 30 hr/nest. Observations were not extended after 2400 H because, prior to this study, we had observed that kestrels roosted as soon as the lights were turned off.

During observations, we recorded instances of young being fed by adults and the sex of the feeder by plumage characteristics (Cramp and Simmons 1980). We tried to identify prey, but deliveries happened so quickly that it was impossible to identify them in most cases. Between 2300–2400 H, we also recorded the maximum number of kestrels that were flying together over the Cathedral and El Salvador, respectively.

Observations were carried out with the help of 40 students of the Faculty of Biological Sciences, University of Seville. They were trained on species recognition and different aspects of breeding biology prior to taking observations. They carried out observations in groups of two and were randomly assigned to the four observation spots. Each group observed for an average of 6 hr. At

Table 1. Maximum number of Lesser Kestrels seen flying together each night (2300–2400 H) of the study period in 1998 at the Cathedral and El Salvador in Seville, Spain.

	NO. OF BREEDING PAIRS	NUMBER IN FLIGHT				
		03 JUNE	11 JUNE	17 JUNE	20 JUNE	21 JUNE
Cathedral	70	26	23	22	55	33
El Salvador	25	5	10	19	15	21

least one of us was present with each student group to supervise fieldwork.

Differences in feeding rates were not significant between the two churches (one-way analysis of variance [ANOVA], $P > 0.05$), so data for the 12 focal nests were pooled for analysis. Differences in feeding rates (feedings/hr) during the time periods were also tested using a one-way ANOVA. For this analysis, we used all observed feedings, including those instances in which the sex of the feeder was unknown. To test for differences in feeding rates between males and females along the different time periods, a two-way ANOVA was used. Period and sex were used as factors, and the analysis was restricted to those observations where the sex of the feeding parent was known.

RESULTS

Lesser Kestrels were active every night we made observations. The number of kestrels that we observed simultaneously while flying at night ranged between 22–55 in the Cathedral, and 5–21 in El Salvador (Table 1). Therefore, a large fraction of birds from each colony was active every night. Kestrels typically soared together in circles over the illuminated buildings. The flock of soaring birds would suddenly disperse and individuals would chase and eat flying insects. Nocturnal flights took place at different heights over both the Cathedral and El Salvador. Often the birds circled and hunted above the Giralda, the Cathedral’s bell tower, which is the tallest structure in the

downtown area with a height of about 98 m. Some kestrels descended to the nests from time to time, although prey deliveries were rarely observed.

A total of 411 prey deliveries were observed at the focal nests, 44 of them during night observation periods. Feeding of nestlings varied significantly between the three daily periods ($F = 25.56$, $df = 2$, $P < 0.001$). On average, we observed 1.3 prey deliveries/hr/nest during midday, 2.1 prey deliveries/hr/nest in the afternoon, and 0.4 prey deliveries/hr/nest during the nocturnal period. A two-way ANOVA showed significant differences between sexes ($F = 7.451$, $df = 1.66$, $P = 0.008$), periods ($F = 31.52$, $df = 2.66$, $P < 0.0001$), and the interaction effect between these two factors ($F = 3.30$, $df = 2.66$, $P = 0.042$). Males provided more food items to the young than females during the day (Fig. 1), as previously reported (Donázar et al. 1992). Nocturnal feedings to young by both males and females were very uncommon

DISCUSSION

We present the first description of nocturnal activity in Lesser Kestrels and examine its possible contribution to the successful raising of young. At the Cathedral and El Salvador, lights used to illuminate the buildings at night attracted large quantities of insects making them both visible and accessible to kestrels. The insects also attracted significant numbers of pipistrelle bats (*Pipistrellus pipistrellus*), which were sometimes found among prey remains of kestrels nesting at the Cathedral (Negro unpubl. data). Bat hunting by Lesser Kestrels is uncommon, and the few published records involved individuals that were hunting at dusk or in daylight (Carbajo and Ferrero 1981, Paterson 1991).

The unusual nighttime activity of Lesser Kestrels included a fairly large fraction of the adults in each colony. In fact, we believe that, at some time, all adult birds in the two colonies were active at night. Kestrels remained active until midnight, when the lights were turned down, approximately 2.5 hr after sunset. Unfortunately, lights did not stay on for the whole night, and we do not know whether the kestrels would be able to extend their activity period even further.

Compared to daytime hours, nest provisioning was minimal at night, so we inferred that the main purpose of the adult kestrels’ activity at night was to feed them-

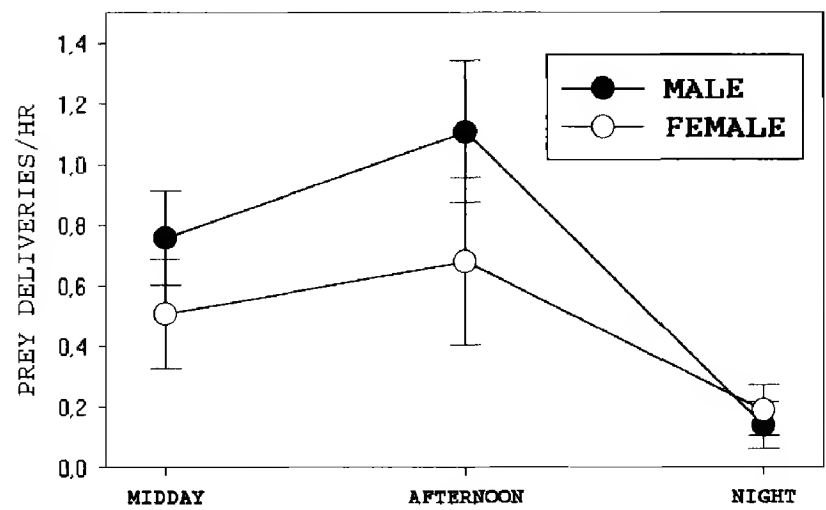


Figure 1. Prey delivery rates ($\bar{x} \pm 2$ SE) by male and female Lesser Kestrels during three periods of observation at the Cathedral and El Salvador in Seville, Spain.

selves. Daytime feeding rates at nests were similar to those found in other areas of southern Spain (2.0 prey deliveries/hr) and Portugal (2.2 prey deliveries/hr), but lower than in rural areas of northern Spain (3.9 feedings/hr) where distances to foraging areas were shorter (Negro 1997).

Lesser Kestrels in Seville breed in colonies in the old downtown area, far from foraging places in the city outskirts. While their nocturnal activity may not result in a significant increase in the prey delivery to the nestlings, it could facilitate feeding of adults during the breeding season perhaps making their urban existence easier (Tella et al. 1995). Urban sprawl around the city is already affecting the hunting areas of the kestrel and it could jeopardize the future of this population. Therefore, nocturnal feeding by the breeding population could make the difference that permits the large kestrel colonies to continue to thrive despite being encroached by many kilometers of apartment blocks in every direction.

Although Lesser Kestrels are typically migratory, some birds remain all year round in southern Spain (Andrada and Franco 1975, González and Merino 1990) and, specifically in Seville (Negro et al. 1991). Andrada and Franco (1974) suggested that nocturnal activity could go on through the year at the Cathedral but it remains to be seen whether wintering kestrels are active at night in Seville.

Further studies are needed to assess the actual effect of nocturnal activity on adult kestrel foraging strategy, not only during the breeding season, but also during the remainder of the year. It is also important to clarify the role of nocturnal foraging in long-term survival in this population.

RESÚMEN.—Estudiamos la actividad nocturna del Cernícalo Primilla (*Falco naumanni*) en dos colonias de cría situadas en edificios históricos del centro de Sevilla (Sur de España). Nuestro objetivo fue describir este comportamiento inusual así como su importancia relativa para la alimentación de los pollos. Se observaron 12 nidos durante tres periodos diarios (1200–1400 H, 1800–2000 H y 2200–2400 H) en Junio de 1998. La mayoría de los cernícalos adultos de ambas colonias estuvieron activos cada noche a lo largo del periodo de estudio mientras funcionaba la iluminación ornamental. La actividad cesaba cuando era apagada la iluminación a medianoche. Los cernícalos capturaban y comían insectos en vuelo llevando pocas presas a los nidos. Los Cernícalos Primillas, por tanto, permanecen activos por la noche para incrementar su ingesta diaria de alimento y no para alimentar a sus pollos. El desarrollo urbanístico de Sevilla está reduciendo los territorios tradicionales de caza de los Cerní-

calos en el entorno de la ciudad. Es posible que la extensión de la caza a horas nocturnas permita que los Cernícalos perduren aún en el centro de Sevilla.

[Traducción de los autores]

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NEST-SITE CHARACTERISTICS OF CRESTED CARACARAS IN LA PAMPA, ARGENTINA

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KEY WORDS: *Crested Caracara*; *Caracara plancus*; nest characteristics; grasslands; Argentina.

Crested Caracaras (*Caracara plancus*) range from the southern United States to southern South America and, although the natural history of North American populations has been described (Bent 1938, Brown and Amadon 1968, Morrison 1996), there has been little in-depth study of the species elsewhere. Nest characteristics for Crested Caracaras have been documented in Baja California (Rivera-Rodriguez and Rodriguez-Estrella 1998), Texas (Dickinson and Arnold 1996), Florida (Morrison 1996), and Argentine Patagonia (Travaini et al. 1994). Knowledge of the Argentine population is limited to Travaini et al. (1994) and several brief notes. In this paper, I describe characteristics of 17 Crested Caracara nests found during December 1998 and January 1999 in northern La Pampa, Argentina, and compare these characteristics with those observed in other populations.

STUDY AREA

The landscape in the northern La Pampa panhandle (approximately 35°14'S, 63°57'W) is dominated by a mix of cattle ranching and row-crop agriculture. Common summer crops are alfalfa, sunflower, sorghum, and corn. Uncommon and isolated native mesquite (*Prosopis* spp.) trees and introduced Chinese elm (*Ulmus parvifolia*) are found along dirt and paved roads. Mesquite trees in fields have generally been removed for agriculture and few remain. Forested areas are generally groves of introduced eucalyptus (*Eucalyptus* spp.) trees, planted as shade areas for cattle, for wind breaks between fields, and as entrance corridors to estate houses. High winds and strong rains are common during the summer, particularly from the southeast. Annual rainfall is 828 mm, with 50% occurring from November through February. Summer temperatures range from 23–38°C.

METHODS

Surveys for caracara nests were conducted by vehicle in December 1998 and January 1999. Surveys were conducted once, over approximately 420 km along a 2000 km² grid of public dirt and paved roads. Roads were buffered by 10 m of public land on each side, were fenced, and lay adjacent to private ranches. Private lands were not surveyed. All trees and shrubs along the roads were checked for caracara nests. Nests showing disrepair or no sign of occupancy during the breeding season were not

used in this analysis. For each occupied nest found (eggs, nestlings, fledglings, or adults at the nest), substrate height (base to the top of substrate), nest height (base to the egg level of the nest), and nest orientation (deviation from magnetic north grouped in 45° octants) were recorded. Nest and nest cup diameters were measured for five nests, two in mesquite and three in elm. Differences in nest heights between tree species were analyzed using a *t*-test. Nest orientation was examined using Rayleigh's test for circular uniformity (Zar 1996). All mean values are presented as mean \pm standard error. A critical value of 0.05 was used for all analyses.

RESULTS AND DISCUSSION

Seventeen caracara nests were found during road surveys. Thirteen nests were found in mesquite and four in elm. Nests were not found in other vegetation types. Nests were generally located in isolated trees and in the tallest vegetation in the immediate area. When nests were found in elms, no mesquite trees were in the vicinity. For two of the nests found in mesquite, a neighboring mesquite tree was located approximately 40 m away. Agricultural fields surrounded all nest trees. Nests were located more than 1 km from the nearest building, although buildings were not generally found near roads, but well inside private estate boundaries. Two nests were located 0.4 km apart.

The average height of the nest tree was 7.4 ± 0.4 m. Mesquite trees containing nests averaged 7.0 ± 1.4 m ($N = 13$) in height; elm trees with nests averaged 8.6 ± 1.7 m ($N = 4$). Mesquite trees were significantly shorter than elms ($t = 1.870$, $df = 15$, $P < 0.05$). Nests were located in the top third of trees, or the upper structural canopy, for both tree species. Nest height in mesquite trees averaged 5.5 ± 1.4 m; nest height in elm trees averaged 6.0 ± 0.8 m. Nest heights between tree species were not significantly different ($t = 0.636$, $df = 15$, $P > 0.05$). The average nest height was 5.6 ± 0.3 m.

Eight nests were oriented towards the northwest and northeast and six nests were oriented towards the southwest (Fig. 1). However, nest orientation did not differ from a uniform distribution (Rayleigh's $R = 3.808$, $N = 17$, $P > 0.05$).

Nests were typically constructed from twigs from the same species of nest tree, woven together with grass stalks. External diameter of nests averaged 58 ± 4 cm in width and 71 ± 6 cm in length. Nest cups averaged 31 ± 1 cm in width and 42 ± 4 cm in length. Internal area accounted for an average of $33 \pm 4\%$ of the nest area. The nest cup was lined with wool, grass, black baling

¹ Present address: Mendocino Redwood Company, P.O. Box 489, Fort Bragg, CA 95437.

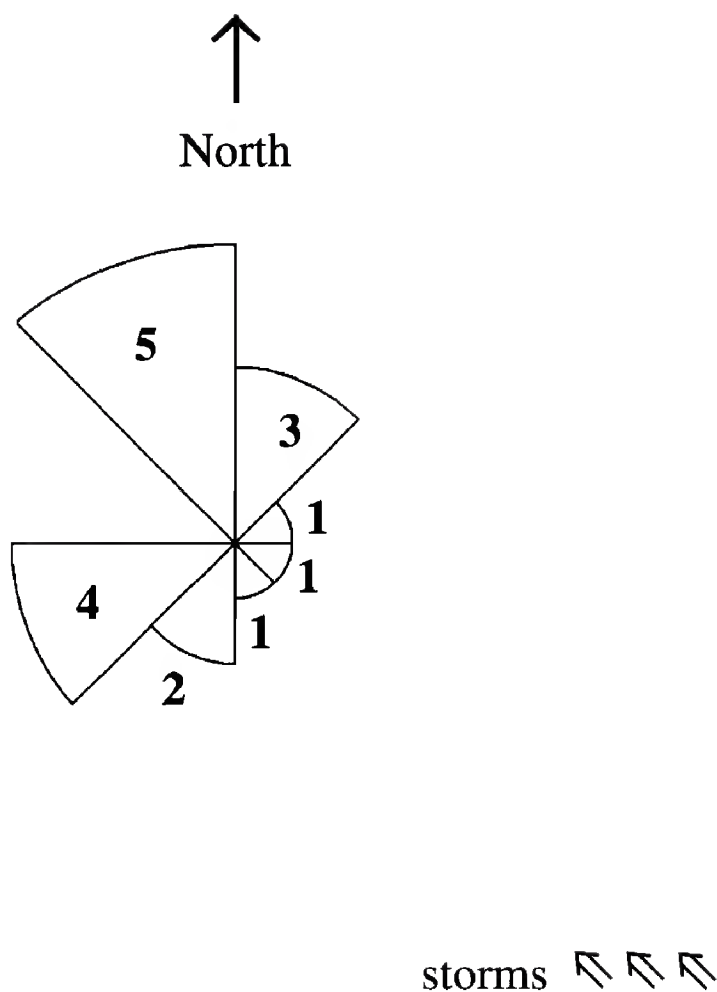


Figure 1. Nest orientation of Crested Caracaras in La Pampa, Argentina. Values are nests open within a 45° sector.

twine, and feathers. Black baling twine was the most common item used to line the nest cup. In one nest, a nestling was found entangled in black baling twine and required extrication. The same nest contained the corpse of a dead nestling with legs entangled in twine. An additional nest contained a dead nestling, also entangled in twine.

The landscape surrounding caracara nests in La Pampa was similar to that described for caracaras nesting in Florida and Texas (Dickinson and Arnold 1996, Morrison 1996); generally open grassland with low ground cover, a low density of tall vegetation, few trees, and scattered brush. Trees in this part of La Pampa have been typically removed from fields; they are found scattered along roadsides, or have been planted for aesthetic beauty, shade or as windbreaks near houses, barns, and corrals. Mesquite trees are more common in the landscape 100-km west in the province of San Luis.

Although mesquite trees used by caracaras were significantly shorter than elms, I obtained neither more detailed measurements of nest tree structure nor data to compare random trees that were not used for nesting. If roadside landscapes are fairly homogenous across this region, choice of the nest tree may be related primarily to structure and cover, not height. In general, mesquite branches are stouter, branch structure is more intertwined, and branches maintain their thorny configura-

tion, thereby providing better structure and cover for caracara nests. Use of elm trees may be related to other structural characteristics or may be a result of the lack of mesquite trees in the vicinity.

Nest dimensions are difficult to measure because nests are frequently reused in consecutive years and become layered in structure and quite large (Bent 1938, Dickinson and Arnold 1996, Morrison 1996). At the end of the nestling period, nestlings stomp the nest flat and it becomes difficult to measure the nest cup or to be sure the peripheral edges of the nest have not deteriorated (Morrison pers. comm.). Nest length in Texas averaged 59 ± 5 cm and nest width averaged 50 ± 2 cm ($N = 5$; Dickinson and Arnold 1996). Florida nests measured 71.1 cm in diameter ($N = 12$; Layne 1996). Nests measured in La Pampa were similar in size.

In both Florida and Patagonia, Crested Caracaras show a strong tendency to orient their nests away from prevailing winds (Travaini et al. 1994, Morrison 1996). During the breeding season in La Pampa, cold storms come from the southeast and warm humid winds come from the subtropical north. Although I found no significant dispersion from random for caracara nests in La Pampa, most nests were generally oriented away from the southeast and towards the north. Since in the Southern Hemisphere the sun crosses the northern sky during the day, the nests facing north are generally facing towards the warm part of the sky and warmer winds.

Across their range, Crested Caracaras use a variety of structural supports for their nests, but typically choose the tallest vegetation available and construct their nests near the top of the nest structure. In Patagonia, nests in aspen (*Populus tremuloides*) were in the lower half of the tree, although nests in *Nothofagus* spp. and *Berberis* spp. were found on top of the substrate (Travaini et al. 1994). In Florida, Texas, and La Pampa, nests were built below the nest-support canopy but tended toward the maximum structural height for the tree species. This suggested some preference for structure or cover in the nest tree, either large enough to support their bulky nests or with cover suitable for protecting young.

In La Pampa, urban growth has proceeded rapidly during the last two decades, resulting in fragmentation of private estates and landscape changes that include persistent loss of native flora. It is reasonable to suspect that the loss of mesquite and other trees resulting from conversion of native vegetation to pasture and agriculture represents loss of breeding structures suitable for use by Crested Caracaras. Although no population data are available for Crested Caracaras in La Pampa, such loss of suitable nest structures may ultimately have a negative influence on the population. Impacts of human activities on these caracaras were also indicated by observations of young becoming entangled in baling twine used to line nests.

RESÚMEN.—Hice un reconocimiento de aproximadamente 2000 km² a través de carreteras asfaltadas y de tier-

Table 1. A comparison of Crested Caracara nest and nest tree heights (mean \pm SE) from several locations across the species' range.

TREE SPECIES	TREE HT (m)	NEST HT (m)	N/T ^b	N	SOURCE ^c
<i>Pachycereus</i> spp.	9.7 \pm 2.2	4.7 \pm 0.8	0.50	18	1
<i>Yucca valida</i>	6.0	4.2	0.71	2	1
<i>Olneya tesota</i>	4.5	4.0	0.89	1	1
<i>Cercidium</i>					
<i>microphyllum</i>	6.0	5.3	0.88	1	1
<i>Washingtonia robusta</i>	9.0	8.5	0.94	1	1
<i>Rosa bracteata</i> ^a	4.3 \pm 1.4	3.7 \pm 1.2	0.86	6	2
<i>Populus tremuloides</i>	19.9 \pm 7.8	8.0 \pm 3.6	0.43	14	3
<i>Maytenus boaria</i>	6.0	4.5	0.76	1	3
<i>Araucaria araucaria</i>	13.0	9.0	0.70	1	3
<i>Berberis darwinii</i>	4.0			1	3
<i>Salix humboldtiana</i>	8.0	4.0	0.50	1	3
<i>Nothofagus</i> spp.	5.0	5.0	1.00	1	3
<i>Sabal palmetto</i>	7.3 \pm 0.2	6.4 \pm 0.2	0.88	83	4
<i>Taxodium distichum</i>	8.5	11	0.77	1	4
<i>Quercus virginiana</i>	8.6	9.3	0.92	1	4
<i>Prosopis</i> spp.	7.0 \pm 1.4	5.5 \pm 1.4	0.79	13	5
<i>Ulmus parvifolia</i>	8.6 \pm 1.7	6.0 \pm 0.8	0.70	4	5
		Mean	0.76		

^a Includes one nest located in yaupon (*Ilex vomitoria*).
^b N/T indicates the ratio of nest height to tree height.
^c Sources: (1) Rivera-Rodriguez and Rodriguez-Estrella 1998, (2) Dickinson and Arnold 1996, (3) Travaini et al. 1994, (4) Morrison pers. comm., and (5) this study.

ra en el norte de La Provincia de La Pampa, Argentina. Encontré 17 nidos de carancho (*Caracara plancus*), 13 en *Prosopis* spp. y 4 en olmos (*Ulmus parvifolia*). El promedio de la altura de los árboles con nidos fue 7.4 m; el promedio de la altura de los nidos fue 5.6 m. Los olmos fueron más altos que los de *Prosopis* spp. (*Ulmus* 8.6 m; *Prosopis* 7.0 m) aunque la altura de los nidos no fué significativamente diferente (*Ulmus* 6.0 m; *Prosopis* 5.5 m). En general, la orientación de los nidos fué distinta a la dirección prevaleciente de los vientos, aunque con la prueba de Rayleigh, no encontré una dispersión significativamente diferente de la normal (Rayleigh's $R = 3.808$, $P > 0.05$). Encontré dos polluelos muertos en nidos en *Ulmus*, con las patas enredadas en cordel de nylon utilizado para embalar pacas de heno. En este reporte, comparé las características de los nidos de carancho en el norte de La Pampa, Argentina, con otras poblaciones de carancho atraves de rango de distribución de esta especie.

[Traducción del autor]

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DIET OF THE BARN OWL (*TYTO ALBA TUIDARA*) IN NORTHWESTERN ARGENTINE PATAGONIA

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KEY WORDS: Barn Owl; *Tyto alba*; diet; Patagonia; Argentina.

Given its wide distribution and sedentary habits, the diet of the Barn Owl (*Tyto alba*) has been studied in more detail and more extensively than that of any other bird of prey (Everett et al. 1992). Rodents and other small mammals are the main prey in the diet of Barn Owl in all of its range along with variable proportions of birds, reptiles, amphibians, fish, and arthropods (Taylor 1994). The Barn Owl (*T. alba tuidara*) is widespread in continental Argentina and occasionally on islands (Canevari et al. 1991). Food habits of the Barn Owl have been thoroughly studied in agrosystems in Argentina (Bellocq 1990, Bellocq and Kravetz 1994), but little is known about its diet in southern Argentina. In Patagonia, most studies have focused on the arid eastern steppes (De Santis and Pagnoni 1989, De Santis et al. 1993, 1996, García Esponda et al. 1998). Our aim was to provide information on the diet of the Barn Owl in a somewhat different area with more mesic vegetation features and a small mammal fauna mixing typical steppe species with others more characteristic of humid forests nearby (Monjeau 1989).

STUDY AREA AND METHODS

The study site was located in the Reserve Area of Nahuel Huapi National Park, in northwestern Argentine Patagonia (71°07'25"W, 40°47'14"S) at 700 m elevation above sea level. The area is an ecotone between the arid Patagonian steppe to the east and the southern beech (*Nothofagus* spp.) forests to the west. The site was dominated by bunchgrasses (*Stipa speciosa*) and cushion bushes (*Mulinum spinosum*) with scattered trees (*Austrocedrus chilensis*, *Maytenus boaria*, and *Populus nigra*). At times, willows (*Salix fragilis*) formed small gallery forests.

Owl roosts were located by observing areas of white-wash or recording places where pellets were found. Pellets were collected every two weeks from June 1993–May 1994 at two known roost sites. Pellets were grouped into calendar seasons, oven-dried in 70°C for 72 hr, and processed following standard methods (Marti 1987). Most prey were identified to species. Mammalian prey were identified and quantified on the basis of skulls and dentaries using reference collections and keys (Pearson 1995). Insects were quantified by counting head capsules and mandibles.

Biomass of each rodent species in the total biomass of the diet was calculated by multiplying mean body mass of individuals by the number of individuals in pellets and expressed as a percentage of total rodent biomass consumed. We calculated the geometric mean of weight of prey (Marti 1987): $GMW = \text{antilog} (\sum n_i \log w_i / \sum n_i)$,

where n_i was the number of individuals of the i th species and w_i was the mean weight. We also determined the mean length of rodents consumed after Jaksic et al. (1977): $MLR = \sum f_i x_i / m$, where f_i was the frequency of the i species in the diet, x_i was mean body length, and m the total number of identified rodents. Mean weight of mammals and mean body length of rodents were taken from the literature (Redford and Eisenberg 1992, Pearson 1995).

Food-niche breadth (FNB) was estimated using Levins' (1968) index: $FNB = 1 / (\sum p_i^2)$, where p_i was the proportion of prey taxon i in the diet. A standardized niche breadth value (FNB_{st}) was then calculated, which ranged from 0–1: $FNB_{st} = (FNB - 1) / (n - 1)$, where n was the total number of prey categories (Colwell and Futuyma 1971). Evenness (J') was calculated by the Shannon-Wiener function as follows: $J' = H' / H'_{max}$, where H' was the Shannon-Wiener function and H'_{max} was the maximum value of H' ; that is, the logarithm of the number of species in the sample (Krebs 1989).

RESULTS AND DISCUSSION

A total of 425 prey items was identified from 229 pellets. The mean number of prey/pellet was 1.9 ± 0.9 (\pm SD, range = 1–4) and the mean number of rodents/pellet was 1.8 ± 0.9 (range = 1–4). Barn Owls preyed mainly on rodents (95.1%). Hares and insects made up 0.5% and 4.4% of prey, respectively. The two European hares (*Lepus europaeus*) found in the diet were newborns. Insects were all in the family Scarabaeidae (Table 1).

By percent frequency, the most consumed sigmodontine rodent species were *Abrothrix longipilis*, *Loxodontomys micropus*, and *Oligoryzomys longicaudatus*. In terms of biomass, *Loxodontomys micropus* was the most important prey in the diet, followed by *Abrothrix longipilis* and *Oligoryzomys longicaudatus* (Fig. 1).

The Barn Owl feeds almost exclusively on small mammals throughout its range, although the proportions of other prey may vary slightly (Taylor 1994). Barn Owls in our study preyed almost exclusively on rodents with juvenile hares and insects rarely appearing in the diet, mostly in spring. We did not find birds, reptiles, nor amphibians to be important prey as was the case in La Pampa, Argentina (Noriega et al. 1993).

Based on the literature, the most important prey of Barn Owls in Argentine Patagonia are *Eligmodontia morgani* and *Reithrodon auritus* (De Santis and Pagnoni 1989, De Santis et al. 1993, Tiranti 1996, Travaini et al. 1997). In our study area, neither species represented >4% and 8% of total prey items, respectively. This was not surprising because the habitat characteristics of our study area

Table 1. Seasonal diet of the Barn Owl in northwestern Argentine Patagonia. *N* = number of prey, % calculated over the total number of prey, and *FNB_{st}* = standardized niche breadth.

PREY	MEAN WEIGHT		SUMMER		AUTUMN		WINTER		SPRING		TOTAL	
	(g)		<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
Mammals												
Rodents												
Muridae												
<i>Abrothrix longipilis</i>	38.2		26	31.3	22	32.4	30	21.6	41	30.4	119	28.1
<i>Abrothrix xanthorhinus</i>	5.3		1	1.2	5	7.4	2	1.4	3	2.2	11	2.6
<i>Eligmodontia morgani</i>	16.6		—	—	6	8.8	3	2.2	5	3.7	14	3.3
<i>Euneomys chinchorilloides</i>	84.7		2	2.4	—	—	1	0.7	—	—	3	0.6
<i>Irenomys tarsalis</i>	44.4		—	—	2	2.9	2	1.4	2	1.5	6	1.4
<i>Loxodontomys micropus</i>	72.8		10	12.1	15	22.1	46	33.1	25	18.5	96	22.7
<i>Oligoryzomys longicaudatus</i>	27.5		14	16.9	2	2.9	28	20.1	20	14.8	64	15.1
<i>Phyllotis xanthopyga</i>	57.5		3	3.6	1	1.5	2	1.4	3	2.2	9	2.1
<i>Reithrodon auritus</i>	81.7		14	16.9	6	8.8	4	2.9	7	5.2	31	7.3
Unidentified			7	8.4	6	8.8	16	11.5	9	6.7	38	8.9
Ctenomyidae												
<i>Ctenomys haigi</i>	164.0		4	4.8	3	4.4	5	3.6	1	0.7	13	3.0
Lagomorphs												
<i>Lepus europaeus</i>			—	—	—	—	—	—	2	1.5	2	0.4
Insects												
Coleopterans			2	2.4	—	—	—	—	17	12.6	19	4.4
Total prey items	83				68		139		135	425		
Total pellets	42				35		82		70	229		
<i>FNB_{st}</i>	0.501				0.486		0.369		0.431	0.415		
Evenness (<i>J'</i>)	0.837				0.843		0.747		0.807	0.802		
No. Prey/pellet	0.98				1.91		1.73		1.90	1.89		
Mean length of rodents (cm)	115.6				114.2		107.2		111.0	113.5		
Geometric mean weight (g)	50.2				44.2		48.1		42.3	46.1		

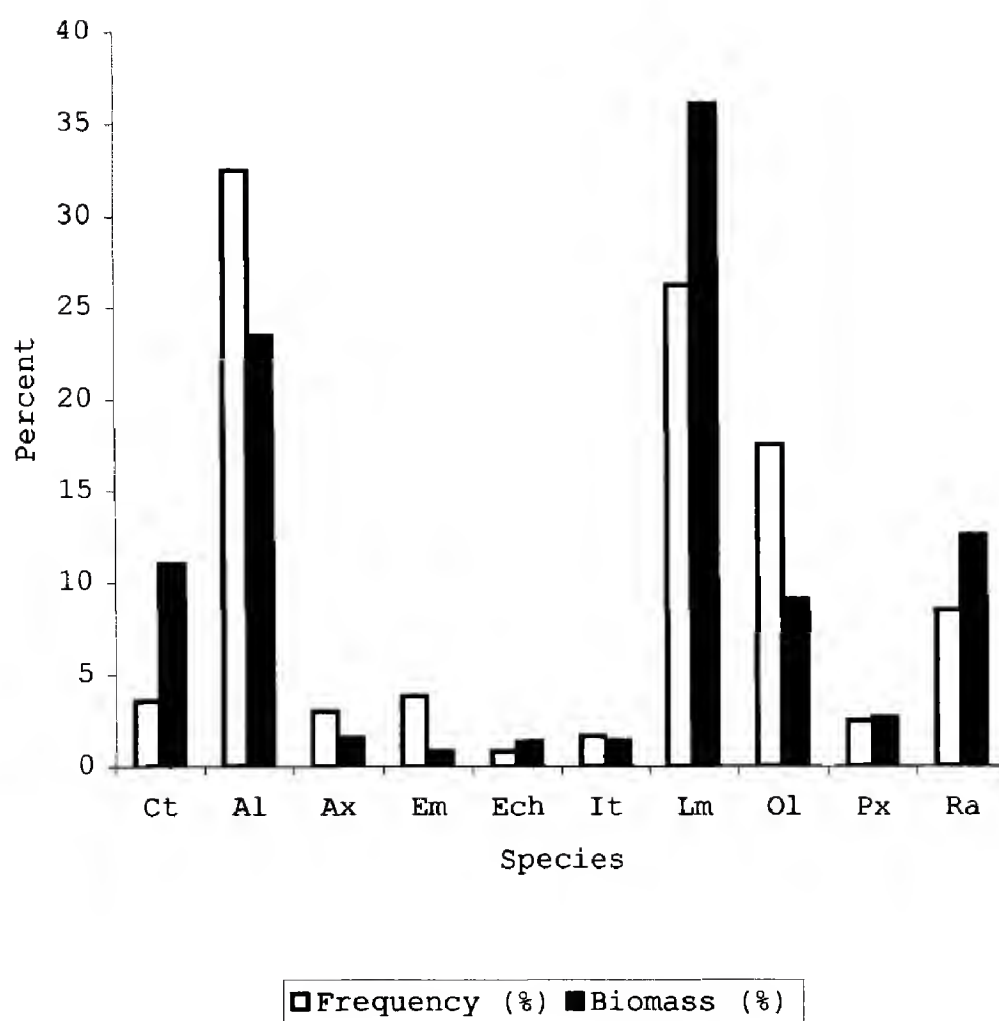


Figure 1. Frequency and biomass of rodent prey species in the diet of the Barn Owl. Biomass is expressed as the percentage of biomass of each species calculated on total rodent biomass. Ct—*Ctenomys haigi*, Al—*Abrothrix longipilis*, Ax—*A. xanthorhinus*, Em—*Eligmodontia morgani*, Ech—*Euneomys chinchilloides*, It—*Irenomys tarsalis*, Lm—*Loxodontomys micropus*, Ol—*Oligoryzomys longicaudatus*, Px—*Phyllotis xanthopyga*, Ra—*Reithrodon auritus*.

were not optimal for these rodents, which prefer the more xeric and open habitats of the Patagonian steppe (Pearson 1995).

The most common species in the diet, both in frequency and biomass, *Abrothrix longipilis*, *Oligoryzomys longicaudatus*, and *Loxodontomys micropus* are good climbers and prefer brushy places, although the latter is also found in shallow wet grasslands (Pearson 1983). Taking this into account, we inferred that the most frequently-used habitats in the Barn Owls' hunting range were those with good vegetation cover and ample water.

Hares were only occasionally eaten by Barn Owls despite their relative abundance (approximately 4–18 hares/ha; Novaro et al. 1992), their crepuscular or nocturnal habits, and their open nests (Bonino and Montenegro 1997), all traits which might make them vulnerable to an aerial nocturnal predator like the Barn Owl. There is only one citation for the Argentine Patagonia recording predation by Barn Owls on rabbits (*Oryctolagus cuniculus*, 0.1% of total prey, Travaini et al. 1997). In central Chile, the proportion of rabbits in the diet of Barn Owls is also very low (0.03% of total prey, Herrera and Jaksic 1980). In Chilean Patagonia, Iriarte et al. (1990) did not record predation on hares by Barn Owls although they were eaten by Great Horned Owls (*Bubo virginianus*) in

variable proportions (Donazar et al. 1997, Trejo and Grigera 1998). Even juvenile hares may not be very suitable prey for Barn Owls since they are much smaller than Great Horned Owls (Everett et al. 1992). According to Jaksic (1986), this is a common situation in southern South America where some predators hunt mainly the more abundant native rodents, often ignoring abundant introduced lagomorphs. Jaksic (1986) attributed this fact to an "escape in size." Maximum weight of juvenile hares is about 300 g (Bonino and Montenegro 1997), which puts them beyond the size of prey more frequently consumed by Barn Owls. Rabbits, although smaller than hares, were probably not in our study area.

Mean weights and sizes of rodents were approximately the same during the four seasons, suggesting that in our study area the Barn Owl preyed more upon medium-sized (*A. longipilis*, *L. micropus*, and *O. longicaudatus*) than on the smaller-sized (*A. xanthorhinus* and *E. morgani*) rodents in the area. Mean weight of prey of the Barn Owl in Chilean Patagonia is smaller (29.9 g), due to a greater consumption of smaller species (Iriarte et al. 1990).

Food-niche breadth is intermediate, as has been shown in Chilean Patagonia (Iriarte et al. 1990). This indicated that the Barn Owls in our study behaved essentially as specialized rodent predators. Diets of sympatric Great

Horned Owls have been studied in two sites in northwestern Patagonia (Donazar et al. 1997, Trejo and Grigera 1998) and, in both cases, a lower food niche breadth (0.20) was found to be due to lower species evenness in the diet.

RESÚMEN.—En el presente trabajo se estudió la dieta de *Tyto alba tuidara* en el noroeste de la Patagonia argentina. Los roedores sigmodontinos fueron el componente principal de la dieta, tanto en número como en biomasa. Las liebres y los insectos fueron poco consumidos. Las especies de roedores más consumidas fueron *Abrothrix longipilis*, *Loxodontomys micropus* y *Oligoryzomys longicaudatus*. De los datos de la dieta y teniendo en cuenta los hábitats de las presas se infiere que la actividad de caza de *T. alba* en el área de estudio se desarrolló preferentemente en ambientes húmedos o mésicos con buena cobertura vegetal. [Traducción de los autores]

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LETTERS

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DIET OF BREEDING NORTHERN GOSHAWKS IN THE COAST RANGE OF OREGON

Northern Goshawks (*Accipiter gentilis*) were not known to breed in the Coast Range of western Oregon until June 1995, when two breeding pairs were reported (Thraill and Andrews 1996, *J. Raptor Res.* 30:248–249). Research suggests that Northern Goshawks generally nest in areas with high prey densities, that they forage opportunistically, and that their diets reflect the diversity of available prey species (Opdam 1975, *Ardea* 63:30–54; Hantage 1980, *J. Ornithol.* 121:200–201; Widen et al. 1987, *Oikos* 49:233–235; Kenward and Widen 1989, Pages 561–567 in B.-U. Meyburg and R.D. Chancellor [Eds.], *Raptors in the modern world. World Working Group on Birds of Prey and Owls*, London, U.K.; Boal and Mannan 1994, *Stud. Avian Biol.* 16:97–102). Thirty or more species of birds and mammals are known to be preyed upon by nesting Northern Goshawks; however, no dietary information exists for the Coast Range of Oregon (Block et al. 1994, *Stud. Avian Biol.* 16). The rarity of nesting goshawks in the Coast Range may be attributed to the dense vegetative structure of the area and its negative influence on prey availability (DeStefano and McCloskey 1997, *J. Raptor Res.* 31:34–39). We believe, therefore, it is important to document the diet of these goshawk pairs.

We studied two goshawk nests that were approximately 16.1 km apart. There were three young in one nest and two young in the other. We collected prey remains (i.e., fur, feathers, skeletal parts) from plucking posts (stumps and tree branches in the nest stands), and nests from 7 June through mid-July 1995. Remains were combined and analyzed as a single sample for each nest site. Skeletal keys (Verts and Carroway 1984, *Keys to the mammals of Oregon*, 3rd Ed. Oregon State Univ. Book Stores Inc., Corvallis, OR U.S.A.) and museum collections (Dept. of Fisheries and Wildlife, Oregon State University, Corvallis, OR U.S.A.) were used to identify prey.

We identified 39 prey items, of which 84% were birds and 16% were mammals. Ruffed grouse (*Bonasa umbellus*) remains comprised 45% of total prey and 64% of bird prey items. Other bird species included Steller's Jay (*Cyanocitta stelleri*) (13%), American Robin (*Turdus migratorius*) (13%), Ring-necked Pheasant (*Phasianus colchicus*) (8%), and Mountain Quail (*Oreortyx pictus*) (5%). Mammalian species included Douglas' squirrel (*Tamiasciurus douglasii*) (13%) and mountain beaver (*Aplodontia rufa*) (3%). We made no attempt to calculate biomass composition of the prey.

Our data were consistent with that of other investigations. The variety of prey species was similar to other goshawk studies in the western United States. Avian prey comprised >50% of the diet during the breeding season. Our sample contained a relatively large percentage of avian prey, as much as 20% greater than some other studies (Meng 1959, *Wilson Bull.* 71:169–174, Opdam 1975; Reynolds and Meslow 1984, *Auk* 101:761–779; Bloom et al. 1986, Calif. Dept. Fish and Game, Wildl. Manage. Branch, Adm. Rept. 85-1; Widen et al. 1987; Bull and Homann 1994, *Stud. Avian Biol.* 16:103–105; Reynolds et al. 1994, *Stud. Avian Biol.* 16:106–113; Watson et al. 1998, *J. Raptor Res.* 32:297–305).

We opportunistically collected prey items from plucking posts and nests after fledging took place, but we did not use direct observations to identify prey delivered to nests. The latter method can indicate a larger proportion of mammals in goshawk diets (Boal and Mannan 1994). The most accurate assessment of raptor diets is accomplished through a combination of direct visual observations and collection of prey remains (Marti 1987, *Raptor food habit studies*, Pages 67–80 in B.G. Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [Eds.], *Raptor management techniques manual*. Nat. Wild. Fed., Sci. Tech. Ser. No. 10). Thus, our results may overestimate the proportion of avian prey.

We suggest that the Ring-necked Pheasant in the diet of one of the two pairs of goshawks studied demonstrates the opportunistic foraging behavior of the goshawk. Although it was not observed, we suspect goshawks may have also foraged in agricultural/pastureland approximately 1.2 km from their nest where a hunting club released pheasants. We occasionally observed pheasants on forest roads near the site, so it is possible the pheasants were captured in the forest. Studies conducted in Europe show that pheasants are important goshawk prey. Habitat there consists of small woodlots surrounded by agricultural fields and pastures where pheasants are released (R. Kenward and P. Widen 1989).

The relative absence of breeding goshawks from the Coast Range is well-documented (DeStefano and McCloskey 1997). They suggested three hypotheses to explain the absence of breeding goshawks from the Coast Range of Oregon. The hypothesis we believe most plausible is that the structure of the vegetation may limit prey availability to goshawks and thus prevent nesting, despite potentially suitable nesting substrate and adequate populations of prey. Two observations support this hypothesis. First, the similarity in the variety of prey species we found in this sample

relative to other studies suggests that prey diversity is not a factor which precludes Northern Goshawk nesting in the Coast Range. Second, our field observations and those of other researchers indicate that dense understories are common throughout the Coast Range (Franklin and Dyrness 1973, Natural vegetation of Oregon and Washington. USDA For. Serv. Tech. Rep. PNW-8, Portland, OR U.S.A.; Reynolds and Meslow 1984; DeStefano and McCloskey 1997). This dense understory may decrease prey vulnerability to Northern Goshawks, reducing foraging efficiency and breeding success. We suspect that the hypothesized lack of suitable foraging habitat may be a limiting factor contributing to the low breeding density of goshawks in the Coast Range of Oregon.

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FIRST DARK MORPH BROOD OF MONTAGU'S HARRIERS (*CIRCUS PYGARGUS*) IN 14 YEARS IN ITALY

The dark morph of the Montagu's Harrier (*Circus pygargus*) is rare in Eurasia and its ecology and adaptive value is unclear. From 1986–99 (14 yr), I studied an Italian population of Montagu's Harriers in a 120 000 ha study area on the eastern slopes of the Central Apennines. It is the southernmost population on the Adriatic coast with the nearest population 70–80 km to the north. The size of this population has varied between 12–32 pairs annually (\bar{x} = 21.7 pairs).

The dark (melanistic) morph of Montagu's Harrier is relatively frequent in the western portion of the European range. In France and Spain, it varies between 2–5% of all individuals in the passage at Gibraltar (Clarke, 1996, Montagu's Harrier, Harlequin Press, Chelmsford, Essex, U.K.) and, in a population in the province of Burgos in northern Spain, as much as 10% of the population (88 nests examined in 1994–96, Sancho and Ansola Aristondo, 1998, Regulación del carácter "plumaje oscuro" en una población de Aguilucho cenizo (*Circus pygargus*), Abstract, 5° Reunión Ibérica sobre Aguiluchos, Evora, Portugal:11) is melanistic. The same is true in Portugal where as much as 20% of the population is the dark morph in Castroverde (Franco pers. comm.). Dark morphs occur less frequently in eastern and central Europe. Shirihai (1996, The birds of Israel, Academic Press, London, U.K.), for example, reported only 10 dark morphs among thousands of Montagu's Harriers migrating through Israel in the 1970s and 1980s. We have no data for the number of dark morphs migrating at the Messina Strait but, in the migration along the Adriatic coast, no melanistic birds have been observed in three years of observations nor have they been observed at the neighboring Monte Conero site where 286 Montagu's Harriers have been observed (Pandolfi et al., 1998, Migrazione primaverile dei rapaci diurni nel Parco Naturale Regionale del San Bartolo (PS), "59° Congresso Nazionale dell'U.Z.I.," Abstract:43).

The Italian breeding population of Montagu's Harriers appears to belong to the eastern portion of the range in this respect. Indeed, in 13 yr of observations through 1999, I encountered only one melanistic male in 1989, and it was not a breeder but a vagrant seen only for a few days in a breeding site of three pairs. During this time, >1000 adult and young Montagu's Harriers were observed in about 280 nests where nearly 400 young fledged. About 20% of these were nonbreeders and each observation/year was independent. Nevertheless, only this single case of a dark morph was observed (<0.1%).

In the 1999 breeding season, while on a late visit to band and tag harriers, three melanistic, young Montagu's Harriers were observed at a nest on 17 July at Monte della Mattered near Mombaroccio, a known breeding site occupied by the harriers almost every year since 1987. The parents of the three melanistic young were light morphs but all three young in the brood were completely dark, smokey brownish-black, except for the upper tail coverts, which were white as in normal brown juveniles and adult females. This last feature, a white mark at the upper end of the tail, is not normally depicted nor described in most field guides or general ornithological books. Indeed, even the two recent books (Clark, 1999, A field guide to the raptors of Europe, the Middle East and North Africa, Oxford Univ. Press, Oxford, U.K. and Forsman, 1999, The raptors of Europe and the Middle East, T. & A.D. Poyser, London, U.K.), make no mention of this white mark on the upper tail coverts.

Sancho and Ansola Aristondo (1998 and pers. comm.) found no melanistic young produced from normal plumage adults. For this reason, they felt the dark plumage character was dominant. Sage (1962, *Br. Birds* 55:201–225) felt

that melanism was a heterozygous dominant trait. The three dark Montagu's Harrier young we observed conflicted with this assessment. Perhaps, the nestlings in the brood resulted from extra pair copulations with a nonbreeding, melanistic male. During the 1999 breeding season, the Monte della Mattered site was monitored three times/wk with a mean of 5.5 hr of observation/d. Useful copulations can occur only during a female's fertile period which, for the Montagu's Harrier, is about 10 d; 7 d before the deposition of the first egg and ending about 1 d before deposition of the last egg (Pandolfi et al., 1998, *J. Raptor Res.* 32:269–277). During the 4-wk courtship period, which includes the fertile period, we made 65 hr of direct, on-site observations of the pair, but no melanistic bird was observed. In all the other breeding sites of the population (a total of 17 pairs recorded and 8–10 nonbreeding harriers), no melanistic individual was observed up to the departure of all birds on migration (first half of August). Extra-pair copulations in Montagu's Harriers seem to be low. In fact, in the population we studied, they were recorded during only 3.4% of the copulations we observed (Pandolfi et al. 1998), while Arroyo has recorded 4–8% in Spain (Arroyo, 1999, *Condor* 101:340–346). Considering these data, it does not seem very likely, although it is remotely possible, that a single vagrant, dark male arrived in this heavily-monitored area during the breeding period, copulated with the female of an existing pair, and immediately left the territory vanishing.

I would like to thank B. Arroyo, K. Bildstein, and an anonymous referee for improving the earlier version of this manuscript and for their helpful suggestions.—**Massimo Pandolfi, Istituto di Scienze Morfologiche, Laboratory of Zoology, University of Urbino, 61029 Urbino, Italy.**

BOOK REVIEW

EDITED BY JEFFREY S. MARKS

J. Raptor Res. 34(4):342

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Raptors at Risk. Edited by R.D. Chancellor and B.-U. Meyburg. 2000. Proceedings of the V World Conference on Birds of Prey and Owls. World Working Group on Birds of Prey and Owls, Berlin, Germany, and Hancock House Publishers, Blaine, WA. 895 pp., numerous figures and tables. ISBN 0-88839-478-0. Paper, \$50. The V World Conference on Birds of Prey and Owls was held in Johannesburg, South Africa, from 4 to 11 August 1998. Organized by the World Working Group on Birds of Prey and Owls (WWGBP), the Raptor Conservation Group, and the Vulture Study Group of the South African Endangered Wildlife Trust, the conference was attended by more than 250 participants. Of the 130 oral presentations and 35 posters presented at the meeting, 88 were published in the proceedings.

The papers are organized into 13 sections: "Current Studies of African Raptors" (12 papers); "Biology & Conservation of the Vultures of the World" (nine); "Falcons in Asia and the Middle East" (eight); "Conservation Models for Raptors of the World" (11); "Raptors in Urban Environments" (six); "Understanding Distribution: the Whys and Wherefores of Geographical Ranges of Raptors" (three); "Predation and Feeding Ecology" (seven); "Conservation Biology of the World's Migratory Raptors" (five); "Islands and Raptors" (10); "Impact of Electricity Utility Structures on Raptors" (five); "Biology of Owls with Emphasis on Vocalisations" (five); "Taxonomy, Phylogeny, Developments in Raptor DNA Studies and Other Theoretical Aspects" (four); and "General Studies" (three). As with previous proceedings published by WWGBP, all of the papers are in English, and the covers are graced with beautiful color photographs

(Indian Vulture [*Gyps indicus indicus*] on front, Lesser Spotted Eagle [*Aquila pomarina*] on back).

Space limitations prevent an in-depth review of the proceedings, so I will highlight only a small number of papers. The section devoted to African raptors contains significant new information on Bat Hawks (*Macheiramphus alcinus*) based on time-lapse video recording at a nest in South Africa (T. Harris, A. Kemp, and J. Dunning) and on Henst's Goshawks (*Accipiter henstii*) gleaned from seven nests observed during three breeding seasons in Madagascar (Lily-Arison Rene de Roland). Also of note are the papers by Bill Clark and R.A.G. Davies on taxonomic problems in African falconiforms and by Michael Wink and Hedi Sauer-Gürth on molecular systematics. The section on vultures contains detailed status reviews of species in Africa (P.J. Mundy), Asia (S.M. Satheesan), and Latin America (Marsha Schlee) plus Lloyd Kiff's review of the status of cathartids in North America. Six papers are devoted to Saker Falcons (*Falco cherrug*) in Asia and the Middle East. Owls receive little attention in this volume. The paper on molecular systematics by Michael Wink and Petra Heidrich adds several species to the growing list of taxa whose phylogeny has been evaluated based on mitochondrial DNA. Wink and Heidrich estimate that New World *Otus* (screech-owls) have been separated from Old World *Otus* (scops-owls) for 6–8 million years and suggest that the two groups should be placed in different genera. They also advocate merging *Nyctea*, *Ketupa*, and *Scotopelia* with *Bubo*.

This volume continues the worthy series of proceedings on the world's raptors produced by Chancellor and Meyburg over the years and thus deserves a place in university libraries and in the personal collections of raptor biologists.—**Jeff Marks, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812 U.S.A.**

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JOURNAL OF RAPTOR RESEARCH

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INDEX TO VOLUME 34

BY ELISE VERNON SCHMIDT

The index includes references to general, species, common names, key words and authors. Reference is also made to book reviews, dissertation and thesis abstracts, letters and reviewers. Taxa other than raptors are included where referenced by authors.

A

- Abundance, raptor, 133–136
- Acarina, 210–231
- Accipiter badius*, 249–261
 - brevipes*, 249–261
 - soloensis*, 249–261
- Activity, 93–101
- Aegolius acadicus*, 42–44, 299–304
- Anderson, Stanley H., see Buhler, Matt L.
- Andrews, Lawrence S., see Thraikill, James A.
- Annual fluctuations, 322–326
- Aposematic coloration, 311–318
- Appetite suppressant, 311–318
- Applegate, Roger D., see Williams, Christopher K.
- Aquila chrysaetos*, 48–52
- Argentina, 108–119, 235–237, 237–241, 330–333, 334–338
- Arizona, 270–278
- Arkansas, 26–32
- Arsenault, David P., see Olson, Chad V.
- Asio clamator*, 235–237
 - otus*, 93–101
- Attie, Carole, see Bretagnolle, Vincent Thomas
- Aviles, J. M., J. M. Sanchez and A. Sanchez, Breeding biology of the Eurasian Kestrel in the steppes of southwestern Spain, 45–48

B

- Baja California, 187–195
- Bakaloudis, Dimitris E., Christos G. Vlachos, and Graham J. Holloway, Nest features and nest-tree characteristics of Short-toed Eagles (*Circus gallicus*) in the Dadia-Lefkimi-Soufli forest, northeastern Greece, 293–298
- Balaquit-Ibanez, Gliceria A., see Miranda, Hector C., Jr.
- Banding and marking, 262–269
- Barton, Nigel W. H., Trapping estimates for Saker and Peregrine Falcons used for falconry in the United Arab Emirates, 53–55
- Bednarz, James C., see Garner, Heath D.
- Behavior, 120–125
- Belloq, M. Isabel, A review of the trophic ecology of the Barn Owl in Argentina, 108–119
- Bird, David M., see Nicholls, Michael K.
- Block, William M., see Ganey, Joseph L.

- Bo, Maria S., Sandra M. Cicchino, and Mariano M. Martinez, Diet of breeding Cinereous Harriers (*Circus cinereus*) in southeastern Buenos Aires Province, Argentina, 237–241
- Bo, Maria S., see Isacch, Juan P.
- Bonin, 241–243
- Book Reviews, 153–155, 247–248, 342
- Bortolotti, Gary, see Murza, Gillian L.
- Bortolotti, Gary, see Miller, Michael J. R.
- Breeding, 56–57
 - biology, 299–304
 - diet, 237–241
 - dispersal, 262–269
 - success, 37–41, 67–74, 322–326
- Bretagnolle, Vincent, Thomas Ghestemme, Jean-Marc Thoiollay, and Carole Attie, Distribution, population size and habitat use of the Reunion Marsh Harrier, *Circus m. maillardi*, 8–17
- Bubo bubo*, 232–235, 305–310
- Buhler, Matt L., Jake H. Powell, and Stanley H. Anderson, Golden Eagle pair kills Ferruginous Hawk in Wyoming, 245–246
- Bustamante, Javier, see Juan Jose Negro
- Buteo albigula*, 143–147
 - buteo toyoshimai*, 241–243
 - jamaicensis*, 26–32, 203–209
 - lagopus*, 157–166
 - lineatus*, 18–25
- Buzzard, Ogasawara, 241–243

C

- California, 187–195
 - northwestern, 75–84
- Call, food and contact, 232–235
 - practice, 232–235
- Calling activity, diurnal, 232–235
- Calvo, Jose Francisco, see Carrete, Martina
- Canyonlands, 1–7
- Caracara, Crested, 330–333
- Caracara plancus*, 330–333
- Carpenter, Leslie B., see Lehman, Robert N.
- Carrete, Martina, Jose Antonio Sanchez-Zapata, and Jose Francisco Calvo, Breeding densities and habitat attributes of Golden Eagles in southeastern Spain, 48–52

Cazassus, Helene, see Penteriani, Vincenzo
 Census, occupied nest, 232–235
 Chile, 143–147
 Chubbs, Tony E., Bruce Mactavish, Keith Oram and Perry G. Trimmer, First confirmed breeding records and other incidental sightings of Northern Harriers in Labrador, 56–57
 Cicchino, Sandra M., see Bo, Maria S.
Carcaetus gallicus, 293–298
Circus cinereus, 237–241
 cyaneus, 56–57, 203–209
 m. maillardi, 8–17
 Claremont, Rita M., see Thrailkill, James A.
 Clutch size, 45–48
 Commentary, 62–63
 Condition, 137–142
 Condor, Andean, 33–36
 Contreras-Balderas, Armando J., see Ruiz-Campos, Gorgonio
 Cover type selection, 203–209
 Cropland, 203–209
 CTA, 311–318

D

Dawson, Russell D., see Murza, Gillian L.
 De Vries, Tjitte, and Cristian Melo, First nesting record of the nest of a Slaty-backed Forest-Falcon (*Micrastur mirandollei*) in Yasuni National Park, Ecuadorian Amazon, 148–150
 Density, 203–209, 241–243
 Desert, Great Basin, 133–136
 Mojave, 133–136
 Diet, 42–44, 108–119, 287–292, 334–338
 Diller, Lowell V., see Folliard, Lee B.
 Dispersal, natal, 1–7
 timing, 1–7
 Distribution, 56–57
 winter, 157–166
 Dobler, Frederick C., see Wilson, Ulrich W.
 Doremus, John H., see Marks, Jeffrey S.
 Dzus, Elston H., see Miller, Michael J. R.

E

Eagle, Bald, 167–174, 287–292
 Golden, 48–52
 Philippine, 37–41
 Short-toed, 293–298
 Eagles, 210–231
 Ecuador, 33–36, 148–150
 El Niño, 67–74
 Endangered species, 126–132
 Endemic, 241–243
 Erickson, Richard A., see Patten, Michael A.
 Eucalyptus, 18–25
 European rabbit, 305–310
 Exotic trees, 18–25

F

Falco cherrug, 53–55
 mexicanus, 262–269
 naumanni, 327–329
 peregrinus, 53–55, 67–74, 126–132
 sparverius, 137–142, 203–209, 311–318
 tinnunculus, 45–48, 319–321
 Falcon, Peregrine, 53–55, 67–74, 126–132
 Prairie, 262–269
 Saker, 53–55
 Falconiformes, 210–231
 Falconry, 53–55
 Falcons, 210–231
 Fattorini, Simone, see Salvati, Luca
 Fish-Owl, Tawny, 102–107
 Folliard, Lee B., Kerry P. Reese, and Lowell V. Diller, Landscape characteristics of Northern Spotted Owl nest sites in managed forests of northwestern California, 75–84
 Food choice, 311–318
 habits, 120–125, 167–174, 196–202, 235–237, 287–292
 stress, 305–310
 Foraging, 137–142
 behavior, 327–329
 habitat, 175–186
 Forest, managed, 175–186
 temperate, 143–147
 Forest-Falcon, Barred, 196–202
 Collared, 196–202
 Slaty-backed, 148–150
 Forest fragmentation, 37–41
 Freeman, Pamela L., Identification of individual Barred Owls using spectrogram analysis and auditory cues, 85–92

G

Gallardo, Max, see Penteriani, Vincenzo
 Ganey, Joseph L., William M. Block, and Rudy M. King, Roost sites of radio-marked Mexican Spotted Owls in Arizona and New Mexico: Sources of variability and descriptive characteristics, 270–278
 Garner, Heath D. and James C. Bednarz, Habitat use by Red-tailed Hawks wintering in the delta region of Arkansas, 26–32
 Ghestemme, Thomas, see Bretagnolle, Vincent
 Goldstein, Michael I., Nest-site characteristics of Crested Caracaras in La Pampa, Argentina, 330–333
 Grande, Juan Manuel, see Negro, Juan Jose
 Grasslands, 330–333
 Greece, 293–298
 Grubb, Teryl G., and Roy G. Lopez, Food habits of Bald Eagles wintering in northern Arizona, 287–292

H

- Habitat, 48–52, 279–286
 selection, 102–107
 use, 8–17, 26–32, 93–101
Haliaeetus leucocephalus, 167–174, 287–292
 Handicaps, 137–142
 Harness, Richard, a review of: *Birds and Power Lines*, Edited by Miguel Ferrer and Guyonne F. E. Janss, 1999, 154–155
 Harrier, Cinereous, 237–241
 Northern, 56–57, 203–209
 Reunion Marsh, 8–17
 Harrier-Hawk, Madagascar, 120–125
 Hawk, Grey Frog, 249–261
 Harris', 187–195
 Red-shouldered, 18–25
 Red-tailed, 26–32, 203–209
 Rough-legged, 157–166
 White-throated, 143–147
 Hawks, 210–231
 Henrioux, Fabienne, Home range and habitat use by the Long-eared Owl in northwestern Switzerland, 93–101
 Herremans, Marc, and Michel Louette, A partial post-juvenile molt and transitional plumage in the Shikra (*Accipiter badius*) and Grey Frog Hawk (*Accipiter soloensis*), 249–261
 Herter, Dale R. and Lorin L. Hicks, Barred Owl and Spotted Owl populations and habitat in the central Cascade Range of Washington, 279–286
 Hicks, Lorin L., see Herter, Dale R.
 Holloway, Graham J., see Bakaloudis, Dimitris E.
 Holt, Eric A., see Lederle, Patrick E.
 Home range, 93–101

I

- Ibanez, Jayson C., see Miranda, Hector C., Jr.
 Idaho, 299–304
 Indian Ocean, 8–17
 Individual identification, 85–92
 Interbreeding, 279–286
 Irwin, Larry L., Dennis F. Rock, and Gregory P. Miller, Stand structures used by Northern Spotted Owls in managed forests, 175–186
 Isacch, Juan P., Maria S. Bo, and Mariano M. Martinez, Food habits of the Striped Owl (*Asio clamator*) in Buenos Aires Province, Argentina, 235–237

J

- Johnston, David W., see Whalen, David M.

K

- Kato, Yuka, see Suzuki, Tadashi
 Kennedy, Patricia L., a review of: *The Northern Goshawk:*

- Ecology, Behavior and Management in North America*, By Thomas Bosakowski, 1999, 153–154
 Kestrel, American, 137–142, 203–209, 311–318
 Eurasian, 45–48, 319–321
 Lesser, 327–329
Ketupa flavipes, 102–107
 King, Rudy M., see Ganey, Joseph L.
 Kochert, Michael N., see Lehman, Robert N.
 Koenen, Marcus T., Koenen, Sarah Gale, and Norma Yanez, An evaluation of the Andean Condor population in northern Ecuador, 33–36
 Koenen, Sarah Gale, see Koenen, Marcus T.

L

- La Marca, Guiseppe, see Thorstrom, Russell
 Labrador, 56–57
 Landscape pattern, 75–84
 Latitudinal segregation, 157–166
 Laying date, 45–48
 Lead exposure, 167–174
 Lederle, Patrick E., James M. Mueller, and Eric A. Holt, Raptor surveys in southcentral Nevada, 1991–1995, 133–136
 Lee, Ching-Feng, see Sun, Yuan-hsun
 Lehman, Robert N., Karen Steenhof, Leslie B. Carpenter, and Michael N. Kochert, Turnover and dispersal of Prairie Falcons in southwestern Idaho, 262–269
 Letters, 58–61, 151–152, 244–246, 339–341
 Lopez, Roy G., see Grubb, Teryl G.
 Louette, Michel, see Marc Herremans
 Love, Oliver P., see Nicholls, Michael K.
 Lutz, R. Scott, see Williams, Christopher K.

M

- Maceda, Juan Jose, see Sarasola, Jose Hernan
 Mactavish, Bruce, see Chubbs, Tony E.
 Managed forest, 75–84
 Manganaro, Alberto, see Ranazzi, Lamberto
 Manganaro, Alberto, see Salvati, Luca
 Manuscript referees, 64
 Margalida, Antoni, see Juan Jose Negro
 Marks, Jeffrey S., Book Reviews, 153–155
 Marks, Jeffrey S. and John H. Doremus, Are Northern Saw-whet Owls nomadic?, 299–304
 Marks, Jeffrey S., a review of *Raptors at Risk*, Ed. By R. D. Chancellor and B.-U. Meyburg, 2000, 342
 Martell, Mark S., Jennifer L. McNicoll and Patrick T. Redig, Probable effect of delisting of the Peregrine Falcon on availability of urban nest sites, 126–132
 Marti, Carl D., a review of *Handbook of the Birds of the World, Volume 5. Barn-owls to Hummingbirds*, Ed. by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal, 1999, 247–248
 Martinez, Mariano M., see Bo, Maria S.
 Martinez, Mariano M., see Isacch, Juan P.

- Mason, J. R., Golden Eagle attacks and kills adult male coyote, 244–245
- McMillan, Anita, see Wilson, Ulrich W.
- McNicoll, Jennifer L., see Martell, Mark S.
- Mediterranean, 48–52, 305–310
areas, 322–326
- Melguizo, Ciro, see Negro, Juan Jose
- Melo, Criatian, see De Vries, Tjitte
- Microstus mirandollei*, 148–150
ruficollis, 196–202
semitorquatus, 196–202
- Middle East, 53–55
- Migration, 42–44, 143–147
differential, 157–166
- Miller, Gregory P., see Irwin, Larry L.
- Miller, Michael J. R., Mark E. Wayland, Elston H. Dzus, and Gary R. Bortolotti, Availability and ingestion of lead shotshell pellets by migrant Bald Eagles in Saskatchewan, 167–174
- Miranda, Hector C., Jr., Salvador, Dennis I., Jayson C. Ibanez, and Gliceria A. Balaquit-Ibanez, Summary of Philippine Eagle reproductive success, 1978–98
- Mites, 210–213
- Molt, contour, 249–261
- Mueller, James M., see Lederle, Patrick E.
- Murza, Gillian L., Gary R. Bortolotti and Russell D. Dawson, Handicapped American Kestrels: Needy or prudent foragers? 137–142

N

- Natal dispersal, 262–269
- Negro, Juan Jose, and Antoni Margalida, How Bearded Vultures (*Gypaetus barbatus*) acquire their orange coloration: A comment on Xirouchakis (1998), 62–63
- Negro, Juan Jose, Javier Bustamante, Ciro Melguizo, Jose Luis Ruiz, and Juan Manuel Grande, Nocturnal activity of Lesser Kestrels under artificial lighting conditions in Seville, Spain, 327–329
- Nest, 56–57
characteristics, 330–333
features, 293–298
first record, 148–150
site fidelity, 262–269
site selection, 75–84
stick, 148–150
tree characteristics, 293–299
- Nesting biology, 120–125
habitat, 175–186
period, 319–321
- Nevada, 133–136
- New Mexico, 270–278
- Niche breadth, 196–202
overlap, 196–202
- Nicholls, Michael K., Oliver P. Love and David M. Bird, An evaluation of methyl anthranilate, aminoaceto-

phenone, and unfamiliar coloration as feeding repellents to American Kestrels, 311–318

Nocturnal activity, 327–329

Nomadism, 299–304

O

- Olson, Chad V., and David P. Arsenault, Differential winter distribution of Rough-legged Hawks (*Buteo lagopus*) by sex in western North America, 157–166
- Olson, Chad V., and Sophie A. H. Osborn, First North American record of a melanistic female Northern Harrier, 58–59.
- Oram, Keith, see Chubbs, Tony E.
- Oregon, 175–186
- Oryctolagus cuniculus*, 305–310
- Osborn, Sophie A. H., see Olson, Chad V.
- Owl, Barn, 108–119, 334–338
Barred, 85–92, 279–286
Eagle, 232–235, 305–310
Long-eared, 93–101
Mexican Spotted, 1–7, 270–278
Northern Saw-whet, 42–44, 299–304
Northern Spotted, 75–84, 175–186, 279–286
Striped, 235–237
Tawny, 322–326
- Owls, 210–231

P

- Palacios, Cesar-Javier, Decline of the Egyptian Vulture (*Neophron percnopterus*) in the Canary Islands, 61
- Pandolfi, Massimo, First dark morph brood of Montagu's Harriers (*Circus pygargus*) in 14 years in Italy, 340–341
- Parabuteo unicinctus*, 187–195
- Paramo, 33–36
- Parasites, 210–231
- Parrish, John W., Possible prevention of European Starling nesting by Southeastern American Kestrels at a power substation in southern Georgia, 152
- Patagonia, 334–338
- Patten, Michael A., and Richard A. Erickson, Population fluctuations of the Harris' Hawk (*Parabuteo unicinctus*) and its reappearance in California, 187–195
- Pavez, Eduardo F., Migratory movements of the White-throated Hawk (*Buteo albigula*) in Chile, 143–147
- Pellet analysis, 42–44, 287–292
- Pellets, 287–292
- Penteriani, Vincenzo, Max Gallardo and Helene Cazasus, Diurnal vocal activity of young Eagle Owls and its implications in detecting occupied nests, 232–235
- Philips, James R., A review and checklist of the parasitic mites (Acarina) of the Falconiformes and Strigiformes, 210–231
- Pillado, Maria S., and Ana Trejo, Diet of the Barn Owl (*Tyto alba tuidara*) in northwestern Argentine Patagonia, 334–338

Pithecophaga jefferyi, 37–41
 Playback, 319–321
 Plumage, transitional post-juvenile, 249–261
Polyboroides radiatus, 120–125
 Population decline, 37–41
 fluctuations, 187–195
 size, 8–17
 structure, 33–36,
 trend, 67–74
 turnover, 262–269
 Populations, 279–286
 Powell, Jake H., see Buhler, Matt L.
 Predation, intraguild, 305–310
 Prey abundance, 26–32
 deliveries, 327–329
 Productivity evaluation, 232–235

R

Radio telemetry, 93–101, 102–107, 270–278
 Ranazzi, Lamberto, Alberto Manganaro, and Luca Salvati,
 The breeding success of Tawny Owls (*Strix aluco*) in
 a Mediterranean area: A long-term study in urban
 Rome, 322–326
 Rangeland, 203–209
 Redig, Patrick T., see Martell, Mark S.
 Redwoods, 75–84
 Reese, Kerry P., see Folliard, Lee B.
 Repeated measures, 270–278
 Reproductive rates, 45–48
 success, 18–25
 Riparian, 18–25
 Rock, Dennis F., see Irwin, Larry L.
 Roost sites, 270–278
 Rottenborn, Stephen C., Nest-site selection and repro-
 ductive success of urban Red-shouldered Hawks in
 central California, 18–25
 Ruiz, Jose Luis, see Negro, Juan Jose
 Ruiz-Campos, Gorgonio and Armando J. Contreras-Bald-
 eras, New northern nesting record of the Peregrine
 Falcon in Baja California, Mexico, 151
 Rusch, Donald H., see Williams, Christopher K.

S

Salvador, Dennis I., see Miranda, Hector C., Jr.
 Salvati, Luca, Alberto Manganaro and Simone Fattorini,
 Responsiveness of nesting Eurasian Kestrels *Falco tin-*
 nunculus to call playbacks, 319–321
 Salvati, Luca, see Ranazzi, Lamberto
 Sanchez, A., see Aviles, J. M.
 Sanchez, J. M., see Aviles, J. M.
 Sanchez-Zapata, Jose Antonio, see Carrete, Martina
 Sarasola, Jose Hernan, Ramon Alberto Sosa, and Juan
 Jose Maceda, A case of nest predation on Turkey
 Vultures nesting in Argentina, 60
 Saskatchewan, 137–142, 167–174
 Seabird colonies, 67–74

Seavy, Nathaniel E., Observations at an Ayres' Hawk-Ea-
 gle nest in Kibale National Park, Uganda, 59–60
 Serrano, David, Relationship between raptors and rabbits
 in the diet of Eagle Owls in southwestern Europe
 Competition removal or food stress?, 305–310
 Shikra, 249–261
 Short Communications, 37–57, 148–150, 232–243, 319–
 338
 Shotshell, lead pellets, 167–174
 Siblicide, 120–125
 Songs, 85–92
 Sosa, Ramon Alberto, see Sarasola, Jose Hernan
 Spain, 45–48
 Sparrowhawk, Levant, 249–261
 Steenhof, Karen, see Lehman, Robert N.
 Steppe habitat, 45–48
 Stomach-content analysis, 42–44
 Strigiformes, 210–231
Strix aluco, 322–327
 occidentalis, 279–286
 o. caurina, 75–84, 175–186
 o. lucida, 1–7, 270–278
 varia, 85–92, 279–286
 Sun, Yuan-Hsun, Ying Wang, and Ching-Feng Lee, Hab-
 itat selection by Tawny Fish-Owls (*Ketupa flavipes*) in
 Taiwan, 102–107
 Survey technique, 319–321
 Surveys, helicopter, 67–74
 roadside, 133–136
 roadside raptor, 157–166
 Suzuki, Tadashi and Yuka Kato, Abundance of the Oga-
 sawara Buzzard on Chichijima, the Pacific Ocean,
 241–243
 Switzerland, 93–101

T

Taste aversion, conditioned, 311–318
 Telemetry, 1–7
 Territory, 102–107
 Thiollay, Jean-Marc, see Bretagnolle, Vincent
 Thorstrom, Russell, The food habits of sympatric forest-
 falcons during the breeding season in northeastern
 Guatemala, 196–202
 Thorstrom, Russell and Guiseppe La Marca, Nesting bi-
 ology and behavior of the Madagascar Harrier-Hawk
 (*Polyboroides radiatus*) in northeastern Madagascar,
 120–125
 Thrailkill, James A., Lawrence S. Andrews and Rita M
 Claremont, Diet of breeding Northern Goshawks in
 the Coast Range of Oregon, 339–340
 Transect, line, 203–209
 Trapping, 53–55
 Trejo, Ana, see Pillado, Maria S.
 Trimmer, Perry G., see Chubbs, Tony E.
 Trophic ecology, 108–119
 niche breadth, 237–241

Tyto alba, 108–119, 334–338

U

Urban nesting, 126–132
Rome, 322–326

V

Van Riper, Charles, see Willey, David W.
Variation, sources of, 270–278
Visual perception, 311–318
Vlachos, Christos G., see Bakaloudis, Dimitris E.
Vocalizatons, 85–92
Vultur gryphus, 33–36
Vulture, 33–36
Vultures, 210–231

W

Wang, Ying, see Sun, Yuan-hsun
Washington, 279–286
Watts, Bryan D., see Whalen, David M.

Wayland, Mark E., see Miller, Michael J. R.
Whalen, David M., Bryan D. Watts, and David W. Johnston, Diet of autumn migrating Northern Saw-whet Owls on the eastern shore of Virginia, 42–44
Williams, Christopher K., Roger D. Applegate, R. Scott Lutz and Donald H. Rusch, A comparison of raptor densities and habitat use in Kansas cropland and rangeland ecosystems, 203–209
Willey, David W., and Charles van Riper III, First-year movements by juvenile Mexican Spotted Owls in the canyonlands of Utah, 1–7
Wilson, Ulrich W., Anita McMillan, and Frederick C Dobler, Nesting, population trend and breeding success of Peregrine Falcons on the Washington outer coast, 1980–98, 67–74
Winter, 26–32
habitat, 287–292
roosts, 287–292

Y

Yanez, Norma, see Koenen, Marcus T.

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CONTENTS FOR VOLUME 34, 2000

NUMBER 1

FIRST-YEAR MOVEMENTS BY JUVENILE MEXICAN SPOTTED OWLS IN THE CANYONLANDS OF UTAH. David W. Willey and Charles van Riper III	1
DISTRIBUTION, POPULATION SIZE AND HABITAT USE OF THE RÉUNION MARSH HARRIER, <i>CIRCUS M. MAILLARDI</i> . Vincent Bretagnolle, Thomas Ghestemme, Jean-Marc Thiollay and Carole Attié	8
NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS OF URBAN RED-SHOULDERED HAWKS IN CENTRAL CALIFORNIA. Stephen C. Rottenborn	18
HABITAT USE BY RED-TAILED HAWKS WINTERING IN THE DELTA REGION OF ARKANSAS. Heath D. Garner and James C. Bednarz	26
AN EVALUATION OF THE ANDEAN CONDOR POPULATION IN NORTHERN ECUADOR. Marcus T. Koenen, Sarah Gale Koenen and Norma Yanez	33
SHORT COMMUNICATIONS	
SUMMARY OF PHILIPPINE EAGLE REPRODUCTIVE SUCCESS, 1978–98. Hector C. Miranda, Jr., Dennis I. Salvador, Jayson C. Ibañez and Glicería A. Balaquit-Ibañez	37
DIET OF AUTUMN MIGRATING NORTHERN SAW-WHET OWLS ON THE EASTERN SHORE OF VIRGINIA. David M. Whalen, Bryan D. Watts and David W. Johnston	42
BREEDING BIOLOGY OF THE EURASIAN KESTREL IN THE STEPPES OF SOUTHWESTERN SPAIN. J.M. Avilés, J.M. Sánchez and A. Sánchez	45
BREEDING DENSITIES AND HABITAT ATTRIBUTES OF GOLDEN EAGLES IN SOUTHEASTERN SPAIN. Martina Carrete, José Antonio Sánchez-Zapata and José Francisco Calvo	48
TRAPPING ESTIMATES FOR SAKER AND PEREGRINE FALCONS USED FOR FALCONRY IN THE UNITED ARAB EMIRATES. Nigel W.H. Barton	53
FIRST CONFIRMED BREEDING RECORDS AND OTHER INCIDENTAL SIGHTINGS OF NORTHERN HARRIERS IN LABRADOR. Tony E. Chubbs, Bruce Mactavish, Keith Oram and Perry G. Trimper	56
LETTERS	58
COMMENTARY	62

NUMBER 2

NESTING, POPULATION TREND AND BREEDING SUCCESS OF PEREGRINE FALCONS ON THE WASHINGTON OUTER COAST, 1980–98. Ulrich W. Wilson, Anita McMillan and Frederick C. Dobler	67
--	----

LANDSCAPE CHARACTERISTICS OF NORTHERN SPOTTED OWL NEST SITES IN MANAGED FORESTS OF NORTHWESTERN CALIFORNIA. Lee B. Folliard, Kerry P. Reese and Lowell V. Diller	75
IDENTIFICATION OF INDIVIDUAL BARRED OWLS USING SPECTROGRAM ANALYSIS AND AUDITORY CUES. Pamela L. Freeman	85
HOME RANGE AND HABITAT USE BY THE LONG-EARED OWL IN NORTHWESTERN SWITZERLAND. Fabienne Henrioux	93
HABITAT SELECTION BY TAWNY FISH-OWLS (<i>KETUPA FLAVIPES</i>) IN TAIWAN. Yuan-Hsun Sun, Ying Wang and Ching-Feng Lee	102
A REVIEW OF THE TROPHIC ECOLOGY OF THE BARN OWL IN ARGENTINA. M. Isabel Bellocq	108
NESTING BIOLOGY AND BEHAVIOR OF THE MADAGASCAR HARRIER-HAWK (<i>POLYBOROIDES RADIATUS</i>) IN NORTHEASTERN MADAGASCAR. Russell Thorstrom and Guiseppe La Marca	120
PROBABLE EFFECT OF DELISTING OF THE PEREGRINE FALCON ON AVAILABILITY OF URBAN NEST SITES. Mark S. Martell, Jennifer L. McNicoll and Patrick T. Redig	126
RAPTOR SURVEYS IN SOUTHCENTRAL NEVADA, 1991–95. Patrick E. Lederle, James M. Mueller and Eric A. Holt	133
HANDICAPPED AMERICAN KESTRELS: NEEDY OR PRUDENT FORAGERS? Gillian L. Murza, Gary R. Bortolotti and Russell D. Dawson	137
MIGRATORY MOVEMENTS OF THE WHITE-THROATED HAWK (<i>BUTEO ALBIGULA</i>) IN CHILE. Eduardo F. Pavez	143
SHORT COMMUNICATIONS	
FIRST NESTING RECORD OF THE NEST OF A SLATY-BACKED FOREST-FALCON (<i>MICRASTUR MIRANDOLLEI</i>) IN YASUNÍ NATIONAL PARK, ECUADORIAN AMAZON. Tjitte de Vries and Cristian Melo	148
LETTERS	151
BOOK REVIEWS. Edited by Jeffrey S. Marks	153

NUMBER 3

DIFFERENTIAL WINTER DISTRIBUTION OF ROUGH-LEGGED HAWKS (<i>BUTEO LAGOPUS</i>) BY SEX IN WESTERN NORTH AMERICA. Chad V. Olson and David P. Arsenault	157
AVAILABILITY AND INGESTION OF LEAD SHOTSHELL PELLETS BY MIGRANT BALD EAGLES IN SASKATCHEWAN. Michael J.R. Miller, Mark E. Wayland, Elston H. Dzus, and Gary R. Bortolotti	167
STAND STRUCTURES USED BY NORTHERN SPOTTED OWLS IN MANAGED FORESTS. Larry L. Irwin, Dennis F. Rock, and Gregory P. Miller	175
POPULATION FLUCTUATIONS OF THE HARRIS' HAWK (<i>PARABUTEO UNICINCTUS</i>) AND ITS REAPPEARANCE IN CALIFORNIA. Michael A. Patten and Richard A. Erickson	187
THE FOOD HABITS OF SYMPATRIC FOREST-FALCONS DURING THE BREEDING SEASON IN NORTHEASTERN GUATEMALA. Russell Thorstrom	196

A COMPARISON OF RAPTOR DENSITIES AND HABITAT USE IN KANSAS CROPLAND AND RANGELAND ECOSYSTEMS. Chrisopher K. Williams, Roger D. Applegate, R. Scott Lutz, and Donald H. Rusch 203

A REVIEW AND CHECKLIST OF THE PARASITIC MITES (ACARINA) OF THE FALCONIFORMES AND STRIGIFORMES. James R. Philips 210

SHORT COMMUNICATIONS

DIURNAL VOCAL ACTIVITY OF YOUNG EAGLE OWLS AND ITS IMPLICATIONS IN DETECTING OCCUPIED NESTS. Vincenzo Penteriani, Max Gallardo, and Hélène Cazassus 232

FOOD HABITS OF THE STRIPED OWL (*ASIO CLAMATOR*) IN BUENOS AIRES PROVINCE, ARGENTINA. Juan P. Isacch, María S. Bó, and Mariano M. Martínez 235

DIET OF BREEDING CINEREOUS HARRIERS (*CIRCUS CINEREUS*) IN SOUTHEASTERN BUENOS AIRES PROVINCE, ARGENTINA. María S. Bó, Sandra M. Cicchino, and Mariano M. Martínez 237

ABUNDANCE OF THE OGASAWARA BUZZARD ON CHICHIJIMA, THE PACIFIC OCEAN. Tadashi Suzuki and Yuka Kato 241

LETTERS 244

BOOK REVIEW. Edited by Jeffrey S. Marks 247

NUMBER 4

A PARTIAL POST-JUVENILE MOLT AND TRANSITIONAL PLUMAGE IN THE SHIKRA (*ACCIPITER BADIUS*) AND GREY FROG HAWK (*ACCIPITER SOLOENSIS*). Marc Herremans and Michel Louette .. 249

TURNOVER AND DISPERSAL OF PRAIRIE FALCONS IN SOUTHWESTERN IDAHO. Robert N. Lehman, Karen Steenhof, Leslie B. Carpenter, and Michael N. Kochert 262

ROOST SITES OF RADIO-MARKED MEXICAN SPOTTED OWLS IN ARIZONA AND NEW MEXICO: SOURCES OF VARIABILITY AND DESCRIPTIVE CHARACTERISTICS. Joseph L. Ganey, William M. Block, and Rudy M. King 270

BARRED OWL AND SPOTTED OWL POPULATIONS AND HABITAT IN THE CENTRAL CASCADE RANGE OF WASHINGTON. Dale R. Herter and Lorin L. Hicks 279

FOOD HABITS OF BALD EAGLES WINTERING IN NORTHERN ARIZONA. Teryl G. Grubb and Roy G. Lopez 287

NEST FEATURES AND NEST-TREE CHARACTERISTICS OF SHORT-TOED EAGLES (*CIRCAETUS GALLICUS*) IN THE DADIA-LEFKIMI-SOUFLI FOREST, NORTHEASTERN GREECE. Dimitris E. Bakaloudis, Christos G. Vlachos, and Graham J. Holloway 293

ARE NORTHERN SAW-WHET OWLS NOMADIC? Jeffrey S. Marks and John H. Doremus 299

RELATIONSHIP BETWEEN RAPTORS AND RABBITS IN THE DIET OF EAGLE OWLS IN SOUTHWESTERN EUROPE: COMPETITION REMOVAL OR FOOD STRESS? David Serrano 305

AN EVALUATION OF METHYL ANTHRANILATE, AMINOACETOPHENONE, AND UNFAMILIAR COLORATION AS FEEDING REPELLENTS TO AMERICAN KESTRELS. Michael K. Nicholls, Oliver P. Love, and David M. Bird	311
SHORT COMMUNICATIONS	
RESPONSIVENESS OF NESTING EURASIAN KESTRELS <i>FALCO TINNUNCULUS</i> TO CALL PLAYBACKS. Luca Salvati, Alberto Manganaro, and Simone Fattorini	319
THE BREEDING SUCCESS OF TAWNY OWLS (<i>STRIX ALUCO</i>) IN A MEDITERRANEAN AREA: A LONG- TERM STUDY IN URBAN ROME. Lamberto Ranazzi, Alberto Manganaro, and Luca Salvati	322
NOCTURNAL ACTIVITY OF LESSER KESTRELS UNDER ARTIFICIAL LIGHTING CONDITIONS IN SEVILLE, SPAIN. Juan José Negro, Javier Bustamante, Ciro Melguizo, José Luis Ruis, and Juan Manuel Grande	327
NEST-SITE CHARACTERISTICS OF CRESTED CARACARAS IN LA PAMPA, ARGENTINA. Michael I. Goldstein	330
DIET OF THE BARN OWL (<i>TYTO ALBA TUIDARA</i>) IN NORTHWESTERN ARGENTINE PATAGONIA. Maria S. Pillado and Ana Trejo	334
LETTERS	339
BOOK REVIEW. Edited by Jeffrey S. Marks.....	342

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2001 ANNUAL MEETING

The Raptor Research Foundation, Inc. 2001 annual meeting will be held on 25–30 October in Winnipeg, Manitoba, Canada. For information about the meeting contact Jim Duncan, Biodiversity program, Wildlife Branch, Manitoba Natural Resources, Box 24, 200 Saulteaux Crescent, Winnipeg, MB R3J 3W3 Canada. Email jduncan@nr.gov.mb.ca.

Persons interested in predatory birds are invited to join The Raptor Research Foundation, Inc. Send requests for information concerning membership, subscriptions, special publications, or change of address to OSNA, P.O. Box 1897, Lawrence, KS 66044-8897, U.S.A.

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RAPTOR RESEARCH FOUNDATION, INC., AWARDS Recognition for Significant Contributions¹

The **Dean Amadon Award** recognizes an individual who has made significant contributions in the field of systematics or distribution of raptors. Contact: **Dr. Clayton White, 161 WIDB, Department of Zoology, Brigham Young University, Provo, UT 84602 U.S.A.** Deadline August 15.

The **Tom Cade Award** recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. Contact: **Dr. Brian Walton, Predatory Bird Research Group, Lower Quarry, University of California, Santa Cruz, CA 95064 U.S.A.** Deadline: August 15.

The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Andersen, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

Recognition and Travel Assistance

The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Patricia A. Hall, 5937 E. Abbey Road, Flagstaff, AZ 86004 U.S.A.**

The **William C. Andersen Memorial Award** is given to the student who presents the best paper at the annual Raptor Research Foundation Meeting. Contact: **Ms. Laurie Goodrich, Hawk Mountain Sanctuary, Rural Route 2, Box 191, Kempton, PA 19529-9449 U.S.A.** Deadline: Deadline established for meeting paper abstracts.

Grants²

The **Stephen R. Tully Memorial Grant** for \$500 is given to support research, management and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Contact: **Dr. Kimberly Titus, Alaska Division of Wildlife Conservation, P.O. Box 20, Douglas, AK 99824 U.S.A.** Deadline: September 10.

The **Leslie Brown Memorial Grant** for \$500–\$1,000 is given to support research and/or the dissemination of information on raptors, especially to individuals carrying out work in Africa. Contact: **Dr. Jeffrey L. Lincer, 1220 Rosecrans St. #315, San Diego, CA 92106 U.S.A.** Deadline: September 15.

¹ Nominations should include: (1) the name, title and address of both nominee and nominator, (2) the names of three persons qualified to evaluate the nominee's scientific contribution, (3) a brief (one page) summary of the scientific contribution of the nominee.

² Send 5 copies of a proposal (≤5 pages) describing the applicant's background, study goals and methods, anticipated budget, and other funding.